# Annals
### of the
# Missouri Botanical Garden

Vol. 34 SEPTEMBER, 1947 No. 3


## MONOGRAPH OF THE NORTH AMERICAN SPECIES OF CORYDALIS[1]


GERALD BRUCE OWNBEY[2]


### Introduction

My attention was attracted to the genus *Corydalis* of the family Fumariaceae some years ago, since it seemed to offer many unsolved problems in the systematic interpretation of various species. The genus had received no special attention from any American botanist since the time of Engelmann and Gray, and the proposal of nearly forty new names for members of the genus in America by Fedde during the early years of the present century had made it imperative that their proper status be determined so that scientific literature no longer would be encumbered with superfluous nomenclatorial terms.

A great volume of herbarium material has been available, in the study of which I have attempted to make full use of classical methods. In addition, it was felt that field studies would help in the understanding of some of the more difficult species. With this in view a six-weeks field trip was made through the western United States during the summer of 1946.

I have attempted to view all species in the light of modern concepts of speciation. Population studies of one species have confirmed the presence of minor measurable differences between inbreeding colonies of this species, even those not widely separated geographically. I also have had opportunity to grow several species under greenhouse conditions and to test the stability of minor variants. Further work along these lines doubtless would do much in clearing up obscure problems not amenable to standard methods of the herbarium taxonomist.



[1] An investigation carried out at the Missouri Botanical Garden and submitted as a thesis in partial fulfillment of the degree of doctor of philosophy in the Henry Shaw School of Botany of Washington University.

[2] Instructor in Botany, University of Minnesota, Minneapolis.


Issued October 31, 1947.

## History of the Genus

Linnaeus[1] included all of the species of fumariaceous plants known to him in the single polymorphous genus *Fumaria*. The subsequent subdivision of this heterogeneous group of plants was left to later authors who attempted to revive names of pre-Linnaean botanists in something resembling their original sense.

The nomenclatorial complications of the generic name *Corydalis* have been investigated by Sprague[2], from whose account the following discussion largely is abstracted. The name has been used in two distinct senses as follows:

(1) *Corydalis* [Knaut, Meth. Pl. 153. 1716; Dill. Cat. Pl. App. 129. *t. 7.* 1719]; Medik. Phil. Bot. **1**:96. 1789. This is *Cisticapnos* Adans. Fam. Fl. **2**:431. 1763 (*Cysticapnos* Gaertn. Fruct. Sem. Pl. **2**:161. *t. 115.* 1791), and is based upon *Fumaria vesicaria* L. This monotypic genus sometimes is united with *Corydalis* Vent., but in the opinion of students of the family, such as Hutchinson and Fedde, it should be retained separately. As the fruit of *Cysticapnos* is inflated and bladder-like, it seems probable that sufficient grounds exist for segregating the species generically from *Corydalis*.

(2) *Corydalis* Vent. Choix de Pl. *t. 19.* 1803. [*Capnoides* Tourn. Inst. Rei Herb. 423. *t. 237.* 1719]; *Capnoides* Adans. Fam. Pl. **2**:431. 1763. Ventenat treated only a single species, *Corydalis fungosa* (*Adlumia fungosa* Greene), which is now universally recognized as a separate genus. The generic name, however, must be credited to Ventenat, even though the single species is referable to *Adlumia*, since the author states in a footnote that his generic concept is founded upon that of Tournefort, who described and figured *Corydalis sempervirens* (as *Capnoides sempervirens*).

Because of the widespread acceptance of the name *Corydalis* in its modern sense, perhaps occasioned by its adoption by de Candolle in his monumental works[3,4], the International Botanical Congress of Vienna conserved it over *Capnoides* Adans., *Cisticapnos* Adans., *Neckeria* Scop., and *Pseudofumaria* Medik. The conservation of *Corydalis* has insured its permanent use, and has precluded the revival of any other generic name which otherwise might supersede it.

## General Morphology

The aerial parts of *Corydalis* are succulent, and annual or biennial in all of our species. The glaucous foliage and finely dissected leaves give a characteristic aspect to the plants.

In distinguishing sections and species, greatest importance is attached to the morphology of the outer petals, stigma, fruits, seeds, and underground parts. An account of the peculiarities of structure and the special terms used in referring to them is given, therefore, in the following discussion.

[1] Linnaeus, Sp. Pl. **2**:700. 1753.
[2] Sprague, in Kew Bull. Misc. Inf. **1928**:351. 1928.
[3] DeCandolle, Reg. Veg. Syst. Nat. **2**:113. 1821.
[4] DeCandolle, Prod. Syst. Nat. **1**:126. 1824.

*Root:* The nature of the root is an important diagnostic character in delimiting sections. In annual, winter annual, and biennial species of Section EUCORYDALIS, an ordinary tap root is present. This often is quite succulent and may be somewhat lignified when the plant reaches maturity. The roots of the perennial species must also be classified as tap roots, although they become fleshy at a very early seedling stage. In *C. pauciflora* of Section PES-GALLINACEUS the mature root is tuberous and ordinarily bifurcate. In Section RAMOSO-SIBIRICAE, the seedlings develop a tuberous swelling the first year. This grows to large proportions during succeeding years and often is crushed and flattened by pressure of the soil.

*Stem:* A rhizome is present only in perennial species of Section RAMOSO-SIBIRICAE. This gives rise apically to the annual stems.

The hollow, annual stems are succulent in all of our species, although sometimes semi-ligneous at the base. They are monopodial in growth except in Section EUCORYDALIS where they predominately are sympodial. The nodes are somewhat abbreviated toward the base.

*Leaves:* In our species of Section RAMOSO-SIBIRICAE only a single leaf is produced annually until the plants reach flowering age. The number produced in Section PES-GALLINACEUS is unknown, but presumably is low. In all members of Section EUCORYDALIS a basal rosette of leaves is developed prior to the development of the flowering stems. Leaves are produced alternately, the later ones often being progressively reduced in size and intergrading imperceptibly into the floral bracts. The larger stem leaves are petiolate and pinnate except in *C. pauciflora* where they are simple and ternately divided. The primary segments are themselves once or twice pinnatifid or incised. The petioles are somewhat expanded at the base, especially those of the larger cauline leaves. A few sheath-like cataphylls sometimes are present at the base of the stem.

*Inflorescence:* The inflorescence is a terminal raceme or panicle, the flowers being crowded at first but becoming more distant during and after anthesis through elongation of the floral axis. The floral bracts offer very little in the way of diagnostic characters. For the most part they are successively smaller from the base to the apex of the floral axis. The uppermost are often extremely minute.

*Flowers: Corydalis* flowers are bilaterally symmetrical. They are dimerous, having two inconspicuous sepals, two laterally placed outer petals, one of which is spurred, and two inner, dorsi-ventrally placed petals opposite the sepals. There is some cohesion but no true fusion of the petal margins at the base. The stamens are arranged in two phalanges of three each, which are opposite the outer, lateral petals. Morphology of all the parts presumably is conditioned to some extent by compression in the bud. Floral structure is quite uniform throughout the genus.

The very much reduced, rudimentary sepals are scarious and fugacious, and function as protective organs only in the early bud stage. Although they are of little diagnostic value, they are described in detail for each species treated in this paper.

The presence of a single spurred petal and the polyspermous fruit are paramount characters in distinguishing the genus *Corydalis* from closely allied genera. The relative size and shape of the spur vary in different species. In measuring the length for this study the distance from the point of attachment of the pedicel to the tip of the spur is taken. The free end of the petal is carinate. This carina is referred to in the following descriptions as the *hood*. It is often provided with a medial exterior fold, the *crest*, and an expanded border of greater or lesser width, the *wing margin*.

The unspurred outer petal is similar to the spurred one with respect to the hood, crest and wing margin. When the flowers are fully developed, the petal sometimes is geniculate immediately posterior to the hood. In Section Ramoso-sibiricae there is a distinct basal gibbosity which probably represents a rudimentary spur.

The two asymmetric inner petals are connate at their apices and enclose the anthers and stigma at anthesis. They consist of an outer broader portion, the *blade*, and a narrower basal portion, the *claw*. Medially, on the outer surface, there is a longitudinal fold which lies between the margins of the outer petals in the bud. In addition, on the exterior basal half of the blade adjacent to the spurred petal, there is another simple longitudinal fold or fleshy protuberance. Morphology of the inner petals ordinarily is not of diagnostic importance below the sectional level.

Each *stamen phalange* consists of three stamens whose filaments are united laterally. The anther of the central stamen is dithecal; those of the outer stamens are monothecal. The phalange opposite the spurred petal is provided with a nectiferous *stamen spur* which extends into the petal spur and is adnate to it for the greater portion of its length. No morphological characters of value in distinguishing species are to be found in the androecium.

Both the stigma and style are persistent. The style is slender, short, and not distinctive in character. The flattened stigma, however, often is quite characteristic. Stigmatic surfaces are located on papillary projections numbering from four to eight in our species. As the projections are somewhat delicate, an unopened flower or large bud should be selected for examination. In these, germinating pollen does not obscure details of structure as it does in older flowers. The nature of the stigma is of considerable diagnostic value, especially in defining sectional lines.

Teratological flowers of the type termed "peloric" have been reported from time to time. I myself have observed two instances of this phenomenon in which both outer petals were spurred.

Cleistogamy in *Corydalis* has been recognized for many years. In *C. micrantha* and *C. pseudomicrantha* the potentiality for cleistogamy is present at all times. In other species it is rare, non-existent, or unrecognized. The problem of self-fertility is well worth investigation. The flowers of all species studied show evidence of germination of the pollen which is clustered around the stigma. Under

such conditions it is difficult to determine just how much self-pollination actually is occurring. Opportunity for cross-pollination is not lacking as witnessed by the large number of insects, both as to individuals and species, that visit *Corydalis* having brightly colored flowers.

*Fruit:* The young fruit is enclosed by the stamen phalanges at anthesis, and is oriented so that the placentae are opposite the inner petals in the dorsiventral plane and the flattened stigma in the transverse plane. When mature, it is a few- to many-seeded, bicarpellate capsule varying in shape from narrowly linear to broadly elliptical, oblongoid or obovoid, and sometimes flattened at the base. Dehiscence is accomplished by separation of the two valvate portions from the two placentae. In Section RAMOSO-SIBIRICAE the valves roll up elastically from the base and the seeds are scattered to a considerable distance from the parent plant.

All American species of the genus fall into two well-defined groups with respect to disposition of the fruit on the pedicel. In Sections RAMOSO-SIBIRICAE and PES-GALLINACEUS the body of the fruit is geniculate at the base and is reflexed to a marked degree upon erect or spreading pedicels. In Section EUCORYDALIS the fruit is not geniculate and is not reflexed except by actual curvature of the pedicel.

The ovules are campylotropous. At a very early stage a comb-like or sheathing caruncle appears near the point of attachment of the funicle. At maturity the caruncle covers a greater or lesser portion of the seed. The testa is seen to be essentially smooth to variously reticulate or muricately decorated when viewed under magnification. The nature of these decorations, as well as gross size of the mature seed, is of importance in specific diagnosis.

A pathological condition in which the fruits become swollen, spongy and sterile is not uncommon in *C. Caseana* and *C. aurea*. Upon examination such abnormal fruits are found to contain an insect larva. The egg of the adult insect apparently is lodged in the young fruit at flowering time; the resultant larva passes through the early stages of its existence enclosed within the tissues of its host. Faulty interpretation of the peculiar fruit developed under these conditions has led to some confusion in terminology.

## GENERIC RELATIONSHIPS

It is not within the scope of this paper to discuss the relative merits of the many genera of the family Fumariaceae. Hutchinson[5] lists eighteen genera from Europe, Asia, Africa and North America, and Fedde[6] proposes one additional genus from Asia. In North America only four genera are represented, namely, *Fumaria, Dicentra, Adlumia,* and *Corydalis*. All of our species of *Fumaria* are weeds introduced from Europe.

The genus *Corydalis*, the largest of the family, includes a heterogeneous aggregate of species all of which, however, have certain fundamental characters in common. The petals are free or essentially so, and the corolla is zygomorphic,

[5]Hutchinson, in Kew Bull. Misc. Inf. **1921**:97. 1921.
[6]Fedde, in Engler & Prantl, Nat. Pflanzenf. ed. 2. **17b**:121. 1936.

having a single spurred petal. These two characters distinguish the genus clearly from *Adlumia*, which has petals united below, both of the outer ones barely saccate at the base, and, furthermore, it is of climbing habit. The genus *Dicentra* has both outer petals equally spurred, but does not differ fundamentally in any other respect from *Corydalis*. The fruit of *Corydalis* is a 2- to many-seeded, dehiscent, bivalvate capsule, while *Fumaria* has an indehiscent, one-seeded fruit.

The distinctions between extra-American genera of the Fumariaceae and *Corydalis* are of like magnitude to those of the American genera. An important element in the family is its naturalness and the equal systematic value of the features characteristic of its included genera.

## Evolutionary Tendencies and Interspecific Relationships

A discussion of evolutionary tendencies often is speculative. The initial assumption generally made is that distant or close genetic relationships are indicated

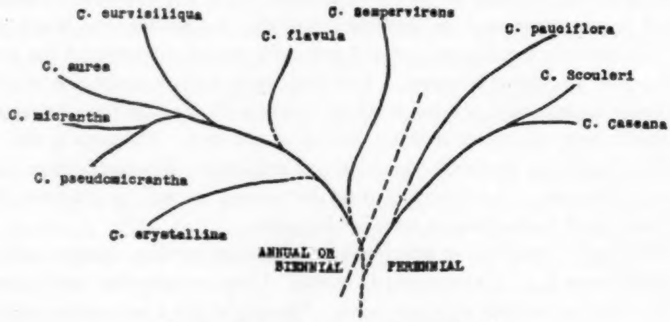



Fig. 1. Suggested interspecific relationships.

by greater or lesser morphological similarities. This assumption ordinarily is justifiable providing due consideration is given to such modifying factors as parallel evolution. Discussions of this nature also are of value in bringing into perspective the probable direction of evolution within the group, and serve to emphasize not only inter-relationships of species, but the characters which are undergoing basic change. This makes possible a prediction of the type of subsequent change to be expected.

Annual species usually are assumed to have arisen from perennial species by compression of the life cycle into a single year. Many genera have both perennial and annual species, *Corydalis* being such a genus. Presumably, one or more lines of perennial species have given rise to the annuals which now predominate in America.

Among perennial species of *Corydalis* are some with rhizomes and some with tuberous roots, one of which type may have given rise to the other at some time in the past. Also, among perennials are species with pinnate leaves and those with sim-

ple, ternately divided leaves. The upper stem leaves of the pinnate-leaved species are much reduced, and, strictly speaking, are simple. Historically, a species with simple leaves could then be derived from one with compound leaves by a foreshortening of the axis or by a reduction of compound leaves to their terminal segments. It is not improbable that this has occurred in *Corydalis*.

Among both perennial and annual species are those with paniculate and those with racemose inflorescences. The racemose type could be derived from a paniculate type by reduction of branching.

In some annual species, such as *C. aurea*, both sympodial and monopodial growth is found. Racemes in both types are terminal. After flowering of the primary raceme in the sympodial type, growth in length is taken over by the uppermost axillary shoot. This in turn gives rise to a terminal raceme. The evolutionary significance of the sympode is not clear. I believe, however, that it should be looked upon as derived from the monopodial type. It may represent only an adaptation for continued growth provided conditions remain favorable.

## Concept of Species and Subspecies

I have attempted to portray the species as natural, biological units, the members of which are more closely related genetically to one another than to members of other species. Closeness of genetic relationship is manifested by relatively close morphological similarities. Comparative morphology, then, remains the most immediately usable criterion of genetic relationship. The individuals of each species are potentially interfertile, or at least their historical progenitors were interfertile. Further, each species occupies a "natural" distribution determined by factors inherent within it.

Great morphological variability in some species of *Corydalis* makes over-all statements of distinguishing characteristics of species and subspecies misleading if unqualified. There apparently is a corresponding amount of genetic diversity in some of these plastic or polymorphic species. *C. aurea*, for example, is relatively uniform throughout the northern part of its range. In southwestern United States it breaks up into innumerable forms or ecotypes. According to recent concepts, these may be looked upon as expressions of genetic differences due to isolation of small segments of the whole. Under such circumstances there is said to be a potential loss of heterozygosity and its accompanying morphological variability, together with potential evolution of the isolated segments along lines divergent from that of the species proper. This appears to be a satisfactory explanation of the condition in *C. aurea*, but experimental data to support this view are insufficient. Although colony-to-colony variation can be demonstrated statistically in *C. flavula*, this does not carry over into any recognizable regional pattern of variability. I hope to have opportunity to discuss this question more fully in a future study.

Another type of variability common to many plant species is most striking in *C. sempervirens* and *C. micrantha*. The conditions under which the particular

plant grows affect gross size and form to a marked degree. For example, plants subjected to abnormally dry conditions often are dwarfed; those growing in shade have fewer branches, more delicate-textured leaves and more slender stems. When plants of *C. micrantha* grow closely crowded together they are less branched and a higher percentage of normal flowers is developed.

The probability of interspecific hybridization in nature is limited to *C. aurea*, *C. micrantha* and *C. curvisiliqua*. These species seem to be closely related, and the possibility or even probability of hybridization among them must be considered. Evidence for this is at present inferential and is based upon plants of intermediate character collected in southern Missouri, Oklahoma, and Texas. Controlled crosses between these species are necessary to supply affirmative or negative evidence of potential hybridization in nature.

In adopting the category of subspecies, I have attempted to maintain its usage in the strictest sense. According to this usage, each subspecies has a discrete or nearly discrete distribution of its own within that of the species as a whole. One may have potential overlap in situations where the habitats favored by the subspecies themselves overlap or intergrade. In instances where two or more elements of the species have been isolated historically by some barrier subsequently removed, the elements may again intermingle along their zone of contact providing they are still interfertile.

The second attribute of a subspecies in *Corydalis* is minor but perceptible morphological differentiation. The subspecies are not always mutually exclusive on morphological grounds, but each has a norm of variability which differs from that of other subspecies. It sometimes becomes a matter of judgment as to whether to describe two closely related elements as species or subspecies. There is no hard-and-fast rule which will be universally applicable due to the fundamental nature of speciation.

## Chromosomal Complements

The basic chromosome number in *Corydalis* is 8 in species, all European, so far reported, with a single exception having a probable basic number of 7. There is evidence of the occurrence of polyploidy in two species, but the data are too scanty to justify generalization.

| Species | Reported by | n | 2n |
|---|---|---|---|
| *C. bulbosa* | Maude[7] | — | 24 |
| *C. cava* | Tischler[8] | 8 | — |
| *C. lutea* | Kellet[9] | — | 56? |
| *C. pumila* | Nemec[10] | — | 16 |

[7] Maude, in New Phyt. 39:18. 1940.
[8] Tischler, in Biol. Centralbl. 48:343. 1928; Planta 8:696. 1939.
[9] Kellet, acc. to Darlington & Janaki, Chromos. Atlas Cult. Pl. p. 69. 1945.
[10] Nemec, acc. to Tischler, in Planta 8:695. 1929.

In two American species which I examined, the diploid number has been tentatively established as 16. I hope that a further report on American species will be possible when data from material now under study are compiled.

## Alkaloidal Properties

The alkaloidal properties of a large number of fumariaceous and papaveraceous species have been reported by Manske[11]. American species of *Corydalis* investigated have been *C. Caseana* (ssp. *Caseana*), *C. Scouleri*, *C. aurea* (ssp. *aurea*), *C. aurea* ssp. *occidentalis* (as *C. montana*), *C. micrantha* (ssp. *australis* ?), *C. crystallina* and *C. sempervirens*. It is of interest to taxonomists that each species was found to contain a particular set of alkaloids, some of which are common to other species but not in the same combinations.

Manske has drawn certain conclusions about interspecific relationships which are substantiated on morphological grounds. For example, from a chemical standpoint, he agrees that *C. micrantha* and *C. crystallina* are species distinct from *C. aurea*. However, he treats *C. aurea* ssp. *occidentalis (C. montana)* as a distinct species, a view that I am not able to support on the basis of comparative morphology. Manske's work has gone a long way in confirming for this group an assumption that perhaps is sometimes unwarranted, that is, that physiological differentiation may accompany morphological differentiation, even in lower systematic categories. It would be of great interest to the taxonomist to know whether changes in alkaloidal properties are present in widely separated geographical segments of a species in which little or no morphological differentiation is present.

## Economic Importance

In so far as is known, the species of *Corydalis* are not of great economic importance. According to collectors' notes, the plants are utilized by the Zuñi Indians of the Southwest, but to what extent or purpose is unknown to me. As a forage for livestock, they are of no importance both because of their relative scarcity and the apparent unpalatibility of the foliage. On account of their high alkaloidal content, it is probable that they are distasteful to livestock as well as toxic if eaten in quantity.

Many species of *Corydalis* have been grown in gardens as much for their value as curiosities as for their intrinsic decorativeness. Of the American species, *C. Caseana* ssp. *Brandegei* and ssp. *Cusickii* are especially recommended for trial. Both are handsome plants in nature, but greatly restricted in habitat. *C. Scouleri, C. aurea,* and *C. sempervirens* have been under cultivation in European gardens in the past.

[11] Series of papers in Can. Jour. Res. Ser. B, beginning with 7:258–264. 1932, and still continuing.

## Geographical Distribution

The genus *Corydalis* is confined almost exclusively to the northern hemisphere. Its center of diversity is in Eurasia, there being several times the number of species there as are found in North America. In North America, the greatest number of species are concentrated in eastern Oklahoma and adjacent Texas, Arkansas, and Missouri, all species found there being placed in Section Eucorydalis. The closest affinities of each of the sections represented in North America are, however, with their Asiatic and European counterparts, and not with each other. Problems of the limits of distribution of the American species are discussed individually in the taxonomic section which follows.

## Acknowledgments

I am greatly indebted to the Missouri Botanical Garden and to its director, Dr. G. T. Moore, for the use of its library and herbarium facilities during the course of this study. I am especially grateful to Dr. J. M. Greenman and Dr. R. E. Woodson for their help and guidance.

I wish to extend my thanks to the curators of the several herbaria who have permitted me to study the material located at their institutions. However, in order to conserve space in this paper it has been necessary to omit detailed lists of specimens examined with the exception of the material from Mexico, Canada, Alaska, and that of *C. micrantha* ssp. *texensis* first described in this paper. The disposition of all numbered and many unnumbered collections viewed in the course of this study may be ascertained by reference to the Index to Exsiccatae. For the information of curators of herbaria and other interested persons, citation of authenticated specimens for each county listed may be found in the original manuscript which is deposited in the library of Washington University, St. Louis, Missouri. Following is a list of the herbaria, together with the abbreviations adopted. Material at each of these herbaria has been viewed and annotated by me.

CA—Herbarium, Colorado Agriculture and Mechanics College.
CAS—Herbarium, California Academy of Sciences.
CIUC—Clokey Herbarium, University of California.
D—Dudley Herbarium, Leland Stanford University.
DU—Herbarium, Duke University.
G—Gray Herbarium, Harvard University.
IH—Intermountain Herbarium, Utah State Agricultural College.
M—Herbarium, Missouri Botanical Garden.
NMA—Herbarium, New Mexico College of Agriculture and Mechanic Arts.
NY—Herbarium, New York Botanical Garden.
RM—Rocky Mountain Herbarium, University of Wyoming.
T—Herbarium, Tulane University.
UA—Herbarium, University of Arizona.

UC—Herbarium, University of California.
UM—Herbarium, University of Minnesota.
UO—Herbarium, University of Oklahoma.
US—United States National Herbarium.
UT—Herbarium, University of Texas.
WS—Herbarium, State College of Washington.

## Taxonomy

CORYDALIS Vent. Choix de Pl. *t. 19.* 1803, *nom. conserv.*, exclusive of *Corydalis fungosa* Vent.; not Medik.

[*Capnoides* Tourn. Inst. Rei Herb. 423, *t. 237.* 1719].
*Fumaria* L. Sp. Pl. 2:700. 1753, in part.
*Capnoides* Adans. Fam. Pl. 2:431. 1763, *nom. rejic.*
*Neckeria* Scop. Introd. Hist. 313. 1777, *nom. rejic.*
*Pseudo-Fumaria* Medik. Phil. Bot. 1:110. 1789, *nom. rejic.*
*Pistolochia* Bernh. Syst. Verz. Pfl. 57. 1800; not Raf.
*Borckhausenia* Gaertn. ex Mey. & Scherb. Oekon.-Tech. Fl. Wett. 3:4. 1801.
*Odoptera* Raf. Cat. 15. 1824.
*Capnites* Dumort. Fl. Belg. 117. 1827.
*Bulbocapnos* Bernh. in Linnaea 8:469. 1833.
*Sophorocapnos* Turcz. in Bull. Soc. Nat. Mosc. $21^1$:570. 1848.
*Cryptoceras* Schott & Kotschy, in Oester. Bot. Wochenbl. 4:121. 1854.
*Corydallis* Aschers. Fl. Prov. Brand. 2:9. 1864.
*Capnodes* Ktze. Rev. Gen. 1:13. 1891.

Annual, biennial or perennial herbs from a tap root, tuberous root or rhizome; stems monopodial or sympodial; leaves simple or pinnate, the pinnae deeply once or twice divided and incised; inflorescence a panicle or raceme, terminal, bracteate; flowers bilaterally symmetrical; sepals 2, scarious, often fugacious; petals 4, free or somewhat coherent at the base, in two whorls of two petals each; outer petals dissimilar, one spurred, the other sometimes gibbous at the base, both more or less distinctly keeled or hooded at the apex; inner petals similar, connate at the apices, clawed; stamens in two groups or phalanges opposite the outer petals, each phalange with three anthers, the outer two of which are monothecal, the central dithecal; phalange opposite the spurred petal having a distinct glandular spur which is adherent to the inner surface of the petal spur except at the tip; stigma persistent, flattened, sometimes 2-lobed, with 4–8 papillary stigmatic surfaces; style distinct, slender; fruit a bicarpellate, many-seeded capsule, with two sterile valves and two persistent placentae; seeds having a distinct chalazal appendage or caruncle, smooth or variously decorated under magnification.

Standard Species: C. SEMPERVIRENS (L.) Pers. Syn. Pl. 2:269. 1807.

### KEY TO THE SECTIONS

A. Perennial from a rhizome or tuberous root; leaf blades pinnate or simple; flowers never yellow; fruits oblongoid to obovoid, reflexed upon erect or spreading, straight pedicels; stigma approximately rectangular or triangular, as long as broad or longer.

B. Rank-growing, hydrophilous species of western United States; rhizome and roots large and fleshy; leaf blades pinnate, the pinnae

once or twice pinnatifid or incised; flowers pink or white; stigma rectangular, or if triangular, narrowest at the apex........Section I. RAMOSO-SIBIRICAE (p. 198)

BB. Low-growing species of the far north; roots small, tuberous, usually bifurcate; leaf blades simple, once ternately divided, the segments incised; flowers blue or purplish-blue; stigma triangular, broadest at the apex ........Section II. PES-GALLINACEUS (p. 207)

AA. Annual or biennial, with a somewhat succulent root; leaf blades pinnate, the pinnae once or twice pinnatifid or incised; flowers yellow (except in sp. 4); fruits narrowly to broadly linear, never reflexed upon the straight or curved pedicels; stigma approximately rectangular, broader than long (except in sp. 4)........Section III. EUCORYDALIS (p. 209)

## SECTION 1. Ramoso-sibiricae (Fedde) G. B. Ownbey, stat. nov.

*Ramoso-sibiricae* Fedde, in Engler & Prantl, Nat. Pflanzenf. ed. 2. **17b**:131. 1936, as subsection.

### KEY TO THE SPECIES AND SUBSPECIES

A. Stem leaves about 3; primary axis of inflorescence with about 25 flowers; flowers pink, the inner petals not tipped with deep red or purple; outer petals having no wing margin, the hood generally having a very high crest; stigma approximately triangular, narrowest at the apex, about as broad as long; fruit obovoid; seeds about 3.5 mm. in diameter, distinctly papillose under magnification; coastal Washington, Oregon, and Vancouver Island........1. *C. Scouleri*

AA. Stem leaves 3–5; primary axis of inflorescence often with 50 or more flowers; flowers pink to white, the inner petals always tipped with deep red or purple; outer petals usually having a well-developed wing margin, the hood with a low or obsolescent crest; stigma approximately rectangular, longer than broad; fruit oblongoid, elliptical, rarely obovoid; seeds about 2.5 mm. in diameter, obscurely papillose under magnification.

B. Plants about 10 dm. tall; wing margin of the outer petals lacking or narrow, the unspurred outer petal acute; California........2. *C. Caseana* ssp. *Caseana*

BB. Plants 8–20 dm. tall (except ssp. 2b); wing margin of the outer petals moderately to very highly developed, the unspurred outer petal not acute.

C. Outer petals rounded, sometimes mucronulate, the wing margin scarcely folded back upon the hood.

D. Plants mostly 10–15 dm. tall; flowers pink or white; outer petals mucronulate; Colorado........2a. *C. Caseana* ssp. *Brandegei*

DD. Plants mostly 4–10 dm. tall; flowers white; outer petals occasionally barely retuse, not mucronulate; Utah........2b. *C. Caseana* ssp. *brachycarpa*

CC. Outer petals emarginate, the wing margin folded back upon the hood.

D. Inflorescence not profusely branched; spurred petal 18–24 mm. long; wing margin very highly developed, not erose; northeastern Oregon and southern Idaho........2c. *C. Caseana* ssp. *Cusickii*

DD. Inflorescence profusely branched; spurred petal 16–20 mm. long; wing margin moderately developed, minutely erose; northern Idaho........2d. *C. Caseana* ssp. *hastata*

As here understood this section includes only two species, *C. Scouleri* of coastal Oregon, Washington, and Vancouver Island, and *C. Caseana* of widespread but sporadic occurrence in many mountainous districts of western United States.

Under *C. Caseana* are included several variants which hitherto have been regarded as distinct species. These variants are essentially identical with respect to coloration of the flowers and detailed morphology of the inner petals, stigmas, fruits, and seeds. They differ appreciably in what are better considered as minor characters, such as the development of a wing margin on the outer petals, length of spur, and length of pedicel. The leaves and gross size of the plants vary to some extent among the different elements of the species, but the taxonomic value of these must be discounted as about the same type and degree of variability are found in other species of the genus.

*Corydalis Caseana* is an excellent example of the type of morphological divergence commonly met with when component parts of a species are isolated geographically. The subspecies might be thought of as incipient species whose modified genetic make-up and consequent morphological divergence have not yet reached the species level. In another sense they might be thought of as remnants of a species which through isolation have lost a large portion of the genetic variability present in the ancient stock.

The members of this section have well-defined habitat requirements, any deviation from which is sufficient to prevent survival. The plants grow in or near a continuous source of fresh, running water, in springs, along small creeks, and in the case of ssp. *Brandegei* also in wet, open, subalpine forests. All require considerable sunlight for best development, but at the same time will tolerate some shade. Plants growing in the sun tend to have smaller, more firmly textured leaves. *C. Scouleri* grows at elevations of sea level to about 2500 feet. The subspecies of *C. Caseana* grow at elevations of 3000–11,000 feet.

The time required for these plants to reach flowering size is not known. At one locality I have seen seedlings of at least three size classes. These classes very likely correspond to age intervals of one year, yet the largest of the seedlings was still relatively small. It therefore seems probable that these plants do not attain flowering size until they are four years or more old.

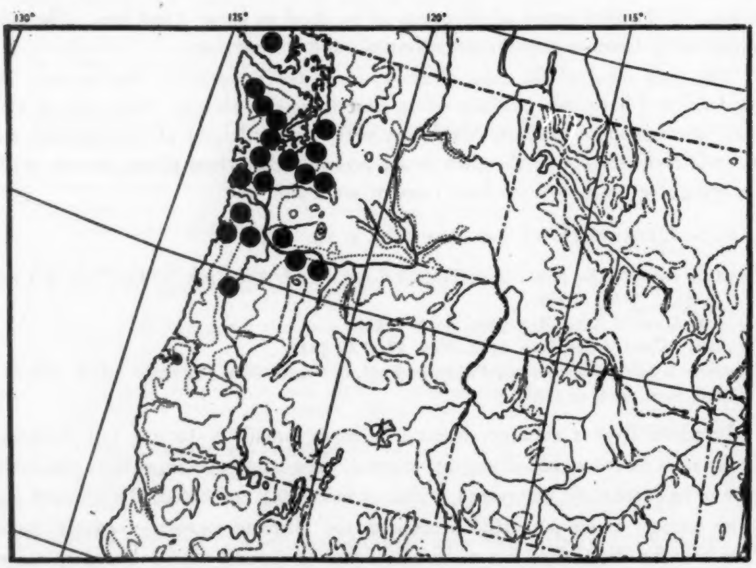
1. C. Scouleri Hook. Fl. Bor. Am. **1**:36. *t. 14.* 1829.

*Corydalis macrophylla* Nutt. apud Torr. & Gray, Fl. N. Am. **1**:69. 1838; Torr. & Gray, l. c. 665. 1840, as syn.
*Capnodes Scouleri* Ktze. Rev. Gen. **1**:15. 1891.
*Corydalis Allenii* Fedde, Rep. Spec. Nov. **10**:478. 1912.
*Capnoides Scouleri* Thornber ex Fedde, in Engl. & Prantl, Nat. Pflanzenf. ed. 2. **17b**:133. 1936, nom. nud. in synon.

Perennial from a rhizome; stems 1 or more, usually 5–10 dm. tall, branched above; stem leaves widely divergent, about 3, very long-petiolate; blades pinnately, more or less ternately, compound, 1 dm. or more long and broad, the primary segments once or twice pinnatifid or incised, the ultimate segments variable, sometimes broadly elliptical or less commonly ovate or obovate with rounded apices, or sometimes narrowly elliptical with acute apices, but more often intermediate, 1–8

cm. long, 0.5–4.0 cm. broad, minutely apiculate; inflorescence not strongly monopodial, consisting of 1 or more simple racemes or sparingly branched panicles arising from the axils of the stem leaves, each raceme usually with fewer than 25 flowers; bracts obscure, the lowermost narrowly elliptical, the upper much reduced, linear; pedicels erect, 2–5 mm. long; sepals ovate or broadly lanceolate, laciniate or toothed, 1–2 mm. long, deciduous at anthesis; flowers light to deep pink, the inner petals not tipped with purple; spurred petal usually somewhat arcuate, 20–25 mm. long, the lanceolate spur 14–20 mm. long, the regular crest moderately to very highly developed, extending to and beyond the acute tip of the hood, wing margin absent; unspurred outer petal 12–15 mm. long, naviculate, the crest similar to that of the spurred petal; inner petals usually 9–11 mm. long, the blade much broader at the apex, the slender claw equalling the blade in length; stamen spur one-half to two-thirds the length of the petal spur, bent or hooked at the apex; stigma roughly triangular, the width at the lower lobes about the same as the length along the medial line; style slender, about 3 mm. long; fruit obovoid, 10–15 mm. long, 4–5 mm. broad; seeds black, about 3.5 mm. in diameter, conspicuously papillose under magnification.

This species is limited in distribution. It is found in wet, cool habitats of northwestern Oregon, northward to Vancouver Island. Morphologically, it is most easily distinguished from *C. Caseana* by its generally highly developed crest and absence of a wing margin on the outer petals. The obovoid fruits most typical of




Map 1. Distribution of *Corydalis Scouleri* Hook.

this species are rarely approached in *C. Caseana,* and its approximately triangular stigma may be contrasted with the nearly rectangular stigma found in that species. Finally, the seeds of *C. Scouleri* are considerably larger and more distinctly papillose.

Within the species there is considerable morphological variability, especially with respect to the leaves. The very small, narrowly elliptical ultimate leaf segments found on some specimens are in part the basis for Fedde's proposed segregate, *C. Allenii,* which I cannot maintain on valid grounds. *C. Scouleri* also is variable with regards to its flowers, particularly in length of spur, amount of curvature of the spurred petal, development of the crest, and gross size. When considered against the background of the species as a whole these variants lose their systematic significance. As possible examples of population variability potentialities of the species from locality to locality they are of considerable interest.

Moist, shady woods, especially along water courses; Vancouver Island, western Washington and northwestern Oregon at elevations of sea-level to about 3500 feet. Flowers about April 15 to June 15; fruits about May 15 to July 30.

BRITISH COLUMBIA: Vancouver Island.

WASHINGTON: Clallam, Clark, Grays Harbor, Jefferson, King, Mason, Pacific, Pierce, Thurston, and Wahkiakum counties.

OREGON: Benton, Clackamas, Clatsop, Columbia, Hood River, Marion, Multnomah, Tillamook, and Washington counties.

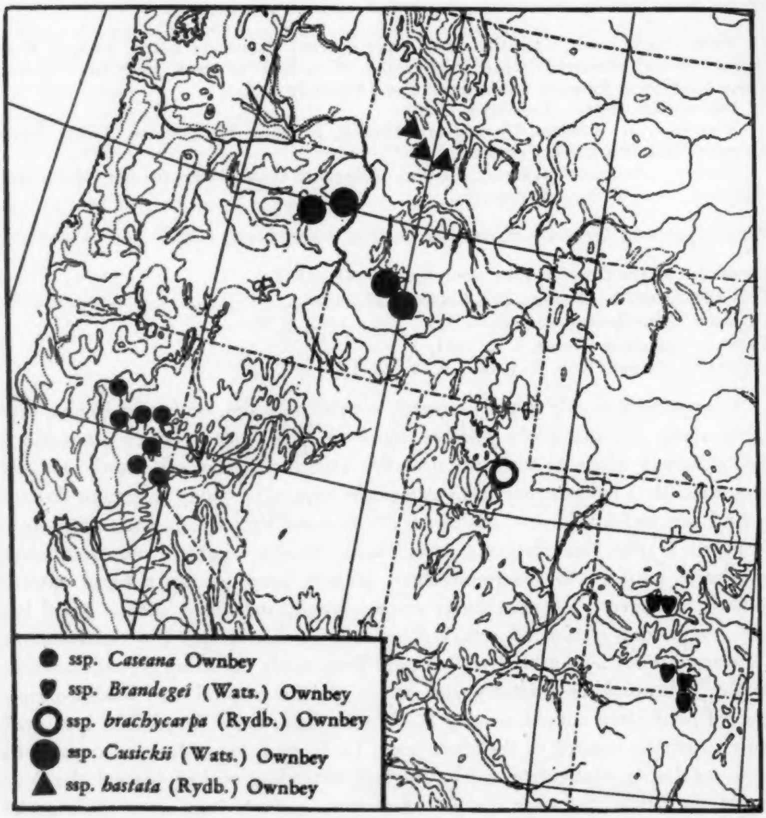
2. C. CASEANA Gray ssp. **Caseana** G. B. Ownbey, stat. nov.

*Corydalis Caseana* Gray, in Proc. Am. Acad. **10**:69. 1874.
*Corydalis Bidwelliae* Watson, Bot. Calif. **2**:429. 1880.
*Capnodes Bidwellianum* Greene, Fl. Fran. 280. 1891.
*Capnodes Caseanum* Greene, l. c. 1891.
*Capnodes Caseanum* Ktze. Rev. Gen. **1**:14. 1891.

Glaucous perennial; stems 1–several, generally 10 dm. or less in height; stem leaves about 5, pinnate, the primary segments again once or twice pinnatifid or deeply incised; ultimate segments narrowly to broadly elliptical, mostly 1–2 cm. long, apiculate; inflorescence paniculate, consisting of a strong numerous-flowered central axis and 1 to several shorter, fewer-flowered lateral axes, these often again branched at the base; bracts inconspicuous, usually narrowly elliptical, rarely broader in outline, the lowermost about 10 mm. long, greatly reduced upward; pedicels semi-erect, 3–5 mm. long; sepals variable, sometimes with a broad base and a very long-attenuated central lobe, sometimes orbicular and denticulate at the margin, sometimes otherwise, 2–4 mm. long, rarely persisting through anthesis; flowers light pink or probably also white, the inner petal tips reddish-purple; spurred petal often curved, usually 16–22 mm. long, rarely longer, the spur gradually to rapidly tapered to the blunt apex, 12–16 mm. long, the hood crested, the crest regular or denticulate, rarely obsolete, extending to and beyond the acute tip of the petals, the wing margin, if present, narrow, regular or more or less denticulate and not folded back toward the hood; unspurred outer petal 10–12 mm. long, the crest and margin similar to that of the spurred petal; inner petals

usually 9–10 mm. long, the claw 3–5 mm. long; stamen spur one-half to three-fourths the length of the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style about 3 mm. long; fruit oblong, 10–15 mm. long, 3–4 mm. broad; seeds dark brown to black, minutely papillose under magnification, about 2.5 mm. in diameter.

Morphologically, the subspecies is best distinguished by its narrow or obsolete wing margin, its generally narrower, curved spurred petal, and acute apices of the outer petals. It is probably most closely similar to ssp. *Brandegei* from which it differs appreciably in the smaller gross size of the plants, smaller flowers, and narrower petal margins. The variant named *C. Bidwelliae* by Watson is of no




Map 2. Distribution of *Corydalis Caseana* Gray.

systematic importance. Leaflet size, petal margin, crest and slenderness of the spur upon which Watson's proposed species was based vary to some extent even at a single locality.

This plant has been collected as far south in California as Truckee, by Sonne, but there are no recent collections from this area.

Very moist, often shady situations, in springs and on gravel bars, in and along streams; southeastern Shasta County southward and eastward to Placer County, California, at elevations of about 4000–6000 feet. Flowers from about June 1 to July 30; fruits from about July 1 to September 1.

CALIFORNIA: Butte, Lassen, Placer, Plumas, Sierra, and Tehama counties.

2a. C. CASEANA Gray ssp. **Brandegei** (Wats.) G. B. Ownbey, stat. nov.

*Corydalis Brandegei* Watson, Bot. Calif. 2:430. 1880.
*Capnoides Brandegei* Heller, Cat. N. Am. Pl. 55. 1898.

Glaucous perennial; stems 1–several, 5–15, mostly 10–15, dm. or more in height; stem leaves about 5, the lowermost sometimes 10 dm. long, pinnate, the pinnae once or twice pinnatifid or deeply incised, the ultimate segments mostly elliptical, 1–5 cm. or more long, apiculate; inflorescence paniculate, consisting of a central numerous-flowered axis and often 1–several fewer-flowered secondary axes, these sometimes again branched; bracts inconspicuous, narrowly elliptical to linear, much reduced and minute upward; pedicels semi-erect, about 5 mm. in length, up to 10 mm. in fruit; sepals 2–3 mm. long, ovate or orbicular, the margin irregularly toothed; flowers light pink to white, the inner petals tipped with deep red or purple, inverted, the spur often nearly upright along the raceme; spurred petal 18–25 mm. long, the spur 12–16 mm. long, the hood crested, the crest low and regular, extending to and beyond the rounded apex of the petal to form a short beak, the wing margin broad, scarcely folded back toward the hood; unspurred outer petal about 12 mm. long, the crest and wing margin similar to that of the spurred petal; inner petals 10–12 mm. long, the claw 4–5 mm. long; stamen spur about two-thirds the length of the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style about 3 mm. long; fruit oblong, 15–18 mm. long, about 5 mm. broad; seeds dark brown to black, about 2.5 mm. in diameter, minutely papillose under magnification.

This subspecies is distinguished most easily on the basis of the wing margin, which is broad, regular, not retuse at the apex, and not appreciably folded back upon the hood as in ssp. *Cusickii* and ssp. *hastata*. It sometimes appears so when the flowers are distorted in pressing. The manner in which the low, regular crest extends beyond the rounded apex is characteristic. Occasionally the spur is nearly erect and the fruits, when mature, reflexed nearly to the pedicels. This situation is found especially in plants from the southern portion of the range.

Subspecies *Brandegei* is very abundant in Colorado from the summit of Wolf Creek Pass, Mineral County, for approximately 4 miles down the west side, at elevations of about 10,000–10,800 feet. Only a few plants are present on the

east side of the pass. At this site the flowers are uniformly pinkish-lavender in color. At similar elevations in Kebler Pass, Gunnison County, the plant also is abundant, especially on the west slope for at least two miles from the summit. The plants are essentially identical to those at Wolf Creek Pass except with respect to flower color. Here there is a preponderance of very light, nearly white-flowered individuals.

Very moist, subalpine situations, especially along water courses, at elevations of about 8,000–11,000 feet; Gunnison and Delta counties, Colorado, southward to northern Rio Arriba County, New Mexico. Flowers from about June 10 to August 10; fruits from about July 10 to September 10.

COLORADO: Archuleta, Conejos, Delta, Gunnison, Hinsdale, and Mineral counties.

NEW MEXICO: Rio Arriba County.

2b. C. CASEANA Gray ssp. **brachycarpa** (Rydb.) G. B. Ownbey, stat. nov.

*Capnoides brachycarpum* Rydb., in Bull. Torr. Bot. Club **34**:426. 1907.
*Corydalis brachycarpa* Fedde, Rep. Spec. Nov. **10**:315. 1912.

Glaucous perennial; stems 1–6, 4–10 dm. tall; leaves 3–5, the lower ones long-petiolate, pinnate, the pinnae once or twice pinnatifid or incised; ultimate leaf segments elliptical, acute at both ends, usually 1–3 cm. long and 0.4–1.0 cm. broad, minutely apiculate; inflorescence paniculate, consisting of a stout central axis and often one or more secondary axes; bracts linear, the lower ones about 15 mm. long, much reduced above; pedicels stout, spreading to semi-erect, about 5 mm. long at flowering time, up to 10 mm. or more long at fruiting time; sepals ovate or broadly lanceolate, more or less undulate or toothed at the margin, 3–5 mm. long, sometimes persisting through anthesis; flowers white, the inner petals tipped with deep red or purple; spurred petal 18–22 mm. long, the spur straight, gradually narrowed to the blunt apex, 9–12 mm. long, the wing margin broad, undulate, stiff, not appreciably folded back toward the hood, rounded at the apex, occasionally barely retuse, the crest obsolescent or lacking; unspurred outer petal 12–14 mm. long, the margin and crest similar to that of the spurred petal; inner petals 9–11 mm. long, the claw about 4 mm. long; stamen spur one-half to two-thirds as long as the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style about 3 mm. long; fruit oblong in outline, about 12 mm. long and 4 mm. broad; mature seeds not seen.

Subspecies *brachycarpa* is a well-marked unit. It is best distinguished morphologically on the basis of the broad, spreading wing margin of the outer petals which are commonly neither acute-tipped nor emarginate, but rounded, at the apex. The broad margin is very well developed even in the bud. The plant possibly is closest to ssp. *Cusickii*, but in addition to the above-mentioned differences, it is only about one-half as large. The leaves are very similar to those of ssp. *Cusickii* as found in Oregon.

The name *brachycarpa* is something of a misnomer if it was intended to call attention to a fruit difference between this and other members of the complex.

The normal fruits, although perhaps smaller than those ordinarily found in other subspecies, are in no way significantly different. It is probable that the name was applied because of a misinterpretation of the swollen fruits very commonly found on living plants. All such fruits examined were found to contain an insect larva, the adult counterpart of which has not been identified. The stimulation of growth of pathogenic tissue results in a globose, spongy, abnormal, sterile fruit. A similar situation is not uncommon in *C. aurea*.

This subspecies is of very limited distribution, and it is possible that the adult population numbers no more than a few hundred individuals.

On gravel bars along stream courses at elevations of about 8500–10,000 feet; Wasatch Mountains, Salt Lake and adjacent Utah counties, Utah. Flowers from about July 1 to July 30; fruits from about July 30 to August 30.

UTAH: Salt Lake and Utah counties.

2c. C. CASEANA Gray ssp. **Cusickii** (Wats.) G. B. Ownbey, stat. nov.

*Corydalis Cusickii* Watson, Bot. Calif. 2:430. 1880.
*Capnoides Cusickii* Heller, Cat. N. Am. Pl. 55. 1898.
*Corydalis Hendersonii* Fedde, Rep. Spec. Nov. 12:278. 1913; not Hemsl.
*Corydalis idahoensis* Fedde, l. c. 16:195. 1919.

Glaucous or green perennial; stems 1–several, 8–15 dm. tall; leaves 4–6, pinnate, the pinnae once or twice pinnatifid or deeply incised; ultimate leaf segments usually narrowly, sometimes broadly, elliptical, apiculate, 1–5 cm. long, 0.5–1.5 cm. broad; inflorescence paniculate, consisting of a stout central axis bearing numerous flowers and 1–several shorter, fewer-flowered secondary axes; lowermost bracts very narrowly to broadly elliptical or obovate, often 15 mm. long, much reduced and usually linear above; pedicels spreading, 5–10 mm. long at flowering time, often up to 15 mm. long at fruiting time; sepals ovate to lunate, often toothed or laciniate, 2–4 mm. long; flowers white or tinged with pink, the inner petals tipped with deep red or purple, the apices of the outer petals widely divergent; spurred petal 18–24 mm. long, the spur generally straight, 10–14 mm. long and not rapidly tapering to the blunt apex, the crest, when present, low and inconspicuous, the wing margin extremely broad, deeply notched at the apex and folded back upon the hood; unspurred outer petal 12–15 mm. long, the margin similar to that of the spurred petal; inner petals 9–11 mm. long, the slender claw about 4 mm. long; stamen spur straight, one-half to three-fourths the length of the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style 3–4 mm. long; fruit oblong-elliptical, 10–15 mm. long, 4–5 mm. broad; seeds dark brown, minutely papillose under magnification, about 2.5 mm. in diameter.

The highest development of the wing margins of the outer petals found anywhere within the species is present in ssp. *Cusickii*. This and the long pedicels are its most distinctive features. The wing margin and emarginate apex is emulated on a much lesser scale by ssp. *hastata*. Both ssp. *brachycarpa* and ssp. *Brandegei* have broad margins, but they never are greatly emarginate at the apex and the

margins are stiffer and never appreciably folded back upon the hood when the flowers are fresh.

This plant was described by Watson from material collected by Cusick in the Wallowa and Blue mountains of northeastern Oregon. It still is collected occasionally in the Wallowa Mts. and is present in some abundance above Cornucopia. It has been collected a few miles above Sumpter in the Blue Mts. and if it is at all abundant in this area it is at this point or further south. In Idaho, a variant with broader bracts, generally broader leaflets, and less-branched inflorescence is common in some localities. The Idaho form was described as *C. Hendersonii* by Fedde. It is found along the tributaries of the South, Middle and North Forks of the Boise River and the South Fork of the Payette River at known elevations of 5000–7500 feet. It does not often occur along the larger streams. On a hillside about 6 miles northeast of Rocky Bar, Elmore County, there is a pure stand covering approximately one-half acre. The plant here reaches its maximum development.

Growing in and along springs and small streams at elevations of about 5000–7500 feet; mountains of southwestern Idaho and northeastern Oregon. Flowers from about June 15 to July 30; fruits from about July 1 to August 15.

IDAHO: Boise, Camas, Elmore, and Valley counties.

OREGON: Baker and Union counties.

2d. C. CASEANA Gray ssp. **hastata** (Rydb.) G. B. Ownbey, stat. nov.

*Capnoides hastatum* Rydb., in Bull. Torr. Bot. Club 34:426. 1907.
*Corydalis hastata* Fedde, Rep. Spec. Nov. 10:315. 1912.
*Corydalis Cusickii* var. *hastata* Fedde, l. c. 12:279. 1913.

Glaucous or green perennial; stems 1–several, 10–18 dm. tall; main stem leaves 3–5, the lower ones widely divergent from the stem, the blade deltoid, pinnate, the pinnae once or twice pinnatifid or deeply incised; ultimate leaf segments broadly elliptical, ovate- or obovate-elliptical, rounded or acute at the ends, usually 1.5–4 cm. long and 0.5–1.5 cm. broad, minutely apiculate, of very thin, tissue-like texture when dry; inflorescence paniculate, delicately and profusely branched, consisting of a main axis and several more or less branched secondary axes; bracts often foliose, ovate to obovate, somewhat reduced above; pedicels about 5 (5–10) mm. long, semi-erect or spreading; sepals about 2 mm. long, usually with an elongate, lanceolate medial lobe and two basal auricles which are often somewhat toothed at the margins; flowers pale pink to white, the inner petals tipped with deep red or purple; spurred petal 16–20 mm. long, the spur 10–12 mm. long, straight or incurved, gradually narrowed toward the broad, blunt apex, the wing margin moderately well developed, reflexed toward the hood, commonly erose, retuse at the apex, the low crest extending over the apex of the hood into a short beak; unspurred outer petal 10–12 mm. long, the margin and crest similar to that of the spurred petal; inner petals 7–9 mm. long, the stout claw about one-third the total length; stamen spur two-thirds to three-fourths as long as the petal spur; stigma approximately rectangular, with 8 papillary stigmatic surfaces; style 2–3

mm. long; fruit oblong, 12–16 mm. long, about 4 mm. broad; mature seeds dark brown, minutely papillose under magnification, about 2.5 mm. in diameter.

Although characterized by numerous morphological differences of greater or lesser value, this plant must be included with *C. Caseana* in the broad sense. It is best distinguished morphologically on the basis of the broadly spreading deltoid leaf blades, the broadly elliptical ultimate leaf divisions, and the profusely branched inflorescence. In floral characters it most closely resembles ssp. *Cusickii*, but differs from it in having considerably smaller flowers with shorter inner petals and outer petals with a much narrower, usually erose wing margin which, as in that subspecies, is reflexed upon the hood and usually is emarginate at the apex. Only in ssp. *Caseana* is the wing margin narrower. The sepals are, indeed, as noted by Rydberg in his original diagnosis, somewhat characteristic. Sepals in *Corydalis* are, however, a very much reduced organ, and there is everywhere considerable variability in outline. I believe that the sepals of ssp. *hastata* cannot justifiably be given much weight as a distinguishing feature.

This subspecies is of limited and as yet not definitely circumscribed distribution. It is found in Idaho from southwestern Shoshone County, southward and eastward to northern Idaho County, probably only at medium elevations. It is especially abundant along Orogrande Creek, Clearwater County. It has been reported from the upper reaches of the Selway River (Moose Creek Trail), but its presence there should be confirmed.

Very wet situations, in and along streams at elevations of about 3000–4000 feet; mountains of northern Idaho. Flowers from about June 15 to July 30; fruits from about July 15 to August 30.

IDAHO: Clearwater, Idaho, and Shoshone counties.

## SECTION II. PES-GALLINACEUS

Sect. PES-GALLINACEUS Irmisch, in Abh. Nat. Ges. Halle 6:273. 1862.

CORYDALIS §. II. *Capnites* DC. Reg. Veg. Syst. Nat. 2:115. 1821.
*Pistolochia* Bernh. Syst. Verz. Pfl. 57. 1800.
*Bulbocapnos* Bernh. in Linnaea 8:469. 1833.

### KEY TO THE SPECIES

A single representative in North America............................................ 3. *C. pauciflora*

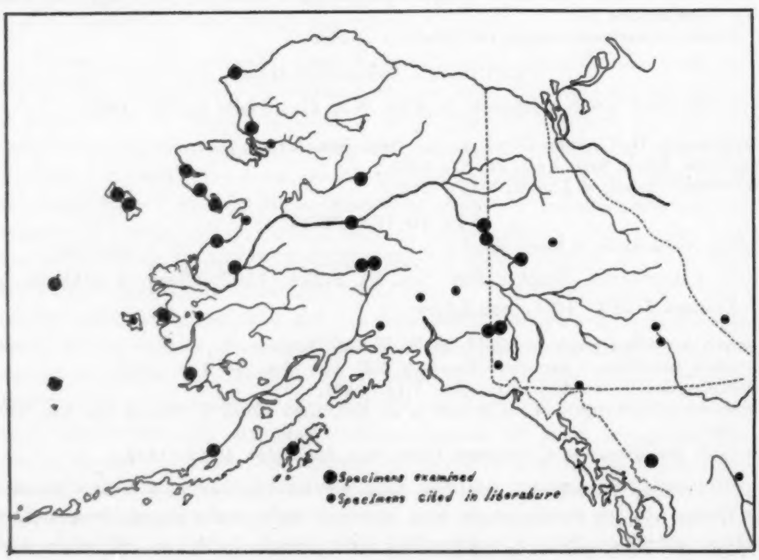
3. C. PAUCIFLORA (Steph.) Pers. Syn. Pl. 2:269. 1807; Cham. & Schlecht. in Linnaea 1:560. 1826, not Edgew.

*Fumaria pauciflora* Steph. ex Willd. Sp. Pl. 3²:861. 1803.
*Corydalis pauciflora* γ *parviflora* Regel, in Bull. Soc. Mosc. 34³:136. 1861.
*Capnodes pauciflorum* Ktze. Rev. Gen. 1:14. 1891.
*Capnoides pauciflorum* Cov. in Brooks et al. Rec. Cape Nome & Norton Bay Reg. 170. 1901.
*Corydalis pauciflora* var. *Chamissonis* Fedde, Rep. Spec. Nov. 16:48. 1919.

Perennial; root deep-set, tuberous, usually bifurcate, having a central channel, the fibrous rootlets mostly at the base, accessory buds at the summit 1–several, or lacking; stems usually 1–3, unbranched, erect, mostly 8–20 cm. tall, often with 1–2 basal cataphylls; basal leaves none; stem leaves 2–5, long-petioled, simple, the

blades ternately divided, the segments again incised into 2–4 (usually 3) lobes, the ultimate lobes elliptical; peduncles stout, terminal, with 3-5 inverted flowers crowded at the summit; bracts ovate to obovate, 4–10 mm. long, 3–5 mm. broad, the lowermost larger; pedicels stout, erect, 4–10 mm. long at flowering time, up to 20 mm. long at fruiting time; sepals scarious, fugacious, 1–2 mm. long and broad, variously toothed; flowers blue, often tinged with purple; spurred petal 17–20 mm. long, the hood short and inconspicuous, the low, regular crest extending to or nearly to the obtuse apex of the petal, the wing margin narrow, the spur 7–10 mm. long, abruptly incurved near the blunt apex; spurless outer petal 10–12 mm. long, nearly as broad basally as apically, the apex 1–2 mm. longer than that of the other petals, the crest similar to that of the spurred petal, the margin reflexed; clawed inner petals 8–10 mm. long, the slender claw occupying one-half or more of the total length, the blade obovate; stamen spur clavate, two-thirds to three-fourths the length of the petal spur; stigma triangular, broadest at the 4-lobed apex; fruits reflexed, about 12 mm. long and 5 mm. broad, elliptical to obovate; seeds turgid, black, shiny, essentially smooth under magnification.

This distinctive species is well known to students of boreal floras. It is the only Asiatic species of *Corydalis* whose distribution extends across the Bering Straits into America. It is beyond the scope of this paper to discuss names proposed for variant forms of the species found in Asia. An excellent discussion of the application of the name to the American plant is to be found in Hultén's recent work (Flora of Alaska and Yukon 5:810. 1945).




Map 3. Distribution of *Corydalis pauciflora* (Steph.) Pers.

In tundra; islands of the Bering Sea and Straits eastward throughout Alaska to the Yukon and northern British Columbia at elevations of sea level to about 3500 feet; also widely distributed in Asia. Flowers from about June 1 to July 15; fruits from about July 1 to August 1.

ALASKA: Ft. St. Michaels, Norton Sound, 1865-66, *Bannister* (G, US); Nome, July, 1890, *Blaisdell 67* (UC); Seal Islands, 1875, *Bryant* (US); Anvik, near the Mission, Lower Yukon River, June 11, 1924, *Chapman 1* (NY); Mission premises, Anvik, without date, *Chapman 28* (G); near Chinik, Seward Peninsula, July 3, 1900, *Collier* (US); St. Paul I., Bering Sea, July 9, 1899, *Coville & Kearney 1810* (US); Port Clarence, July 12, 1899, *Coville & Kearney 1966* (US); Hall I., Bering Sea, July 14, 1899, *Coville & Kearney 2033* (G, US); McKinley Park Sta., Mt. McKinley Nat. Park, June 4, 1932, *Dixon 17* (UC); roadside, Igloo Creek, same locality, June 13, 1932, *Dixon 25* (UC); White River Valley, near the boundary, 1909, *Eaton* (US); St. Matthew I., July 8–13, 1916, *Hanna* (US); on hillside, Goodnews Bay, July 14, 1919, *Harrington 57* (US); St. Paul I., June 30–Aug. 20, 1910, *Heath* (D); Nome, 1914, *Hill 65* (US); wet brook banks, Karluk, June 14, 1901, *Horne* (NY); St. Paul I., Aug. 1, 1897, *Kincaid* (UC); St. Paul I., without date, *MacIntyre* (G); St. Paul I., July, 1892, *Macoun* (NY); St. Paul I., July, 1891, *Macoun* (M, G, US); St. Paul I., June 29, 1914, *Macoun* (NY, US); Cape Lisburne, Aug. 13, 1931, *Mason* (M, UC, NY, G); Iviktook Lagoon, St. Lawrence I., July 10, 1931, *Mason* (UC); Old Man Creek, a branch of the Koyukuk, 4 mi. above camp, near Caribou Mt., July 6, 1901, *Mendenhall* (US); between Yukon River, Nation River, and International Boundary, 1930, *Mertie 60* (US); damp moss in small gulch, open land near Teklanika River, Mt. McKinley Nat. Park, 3600 ft. alt., June 24, 1928, *Mexia 2040* (UC); Golovin Bay, 1881, *Muir 168* (G); moist thicket near headquarters, Mt. McKinley Nat. Park, May 31, 1939, *Nelson & Nelson W-2206* (RM); Nelson I., July 6, 1921, *Palmer 194* (US); St. Paul I., June 10, 1890, *Palmer 178* (US); near Karluk, Kodiak I., June 1, 1897, *Rutter* (D); same locality, May 23, 1897, *Rutter 92* (D); same locality, June 13, 1903, *Rutter 179* (US); same locality, June 14, 1903, *Rutter 206* (M, US); Mt. McKinley Nat. Park, June 13–22, 1937, *Scamman 620* (G); Camp Retreat, June 28, 1886, *Stoney* (US); Anvil Mt., vicinity of Nome, June 29, 1918, *Thornton 319* (US); damp hillside near creek, Tanana, June 14, 1914, *Thousen 6* (DU); St. Paul I., July 9, 1899, *Trelease & Saunders 3872* (M); Hall I., July 4, 1899, *Trelease & Saunders 3873* (M); St. Matthew I., July 15, 1899, *Trelease & Saunders 3874* (M); St. Paul I., July 28, 1895, *True & Prentiss 12* (NY, G, US); Noatak, July, 1929, *Wagner* (US); vicinity of Port Clarence, July 16, 1901, *Walpole 1457* (US); same locality, July 18, 1901, *Walpole 1467* (US); St. Paul I., July, Aug., 1879, *White* (G).

BRITISH COLUMBIA: Mountains near head Iskut River, Cassiar Dist., July 30, 1910, *Preble & Mixter 619* (US).

YUKON: Across Bonanza Creek, Dawson, June 19, 1914, *Eastwood 307* (G, US); 24-mile house, Dawson, June 25, 1914, *Eastwood 380* (CIUC, G, US).

## SECTION III. EUCORYDALIS

Sect. EUCORYDALIS Prantl, in Engler & Prantl, Nat. Pflanzenf. $3^2$:144. 1889.

*Corydalis* §. III. *Capnoides* DC. Reg. Veg. Syst. Nat. 2:122. 1821.

### KEY TO THE SPECIES AND SUBSPECIES

A. Flowers pink, the petals tipped with yellow, the hood not crested, the claw of the inner petals much longer than the blade; stigma not distinctly 2-lobed, with 4 papillary stigmatic surfaces; fruits erect, very slender, usually 30–35 mm. long; seeds about 1 mm. in diameter; Georgia to Newfoundland, British Columbia, and Alaska............ 4. *C. sempervirens*

AA. Flowers pale to bright yellow throughout, the claw of the inner petals equalling or shorter than the blade; stigma 2-lobed, each lobe having 3 papillary stigmatic surfaces; seeds 1.5–2.0 mm. in diameter.

B. Spurred petal 7–9 mm. long, the hood having a high, undulate or toothed crest, the spur incurved, about 2 mm. long; fruits broadly linear, usually straight, pendent on very long pedicels; central to eastern United States........ 5. *C. flavula*

BB. Spurred petal 10–22 mm. long (in normal flowers), the spur not appreciably incurved, usually 4–8 mm. long; fruits erect, on relatively short pedicels (except in sp. 9).

C. Spurred petal 16–22 mm. long, the hood with a very high crest, the wing margin very broad; fruits densely beset with transparent, clavate pustules; southwestern Missouri to central Texas.. 6. *C. crystallina*

CC. Spurred petal 10–18 mm. long, the wing margin moderately broad to narrow; fruits essentially glabrous, although sometimes obscurely granulose along the sutures.

D. Plants often bearing cleistogamous flowers; spurred petal of normal flowers 10–15 mm. long, the hood with a low, regular, undulate or obsolescent crest; seeds about 1.5 mm. in diameter, nearly smooth under magnification.

E. Normal-flowered racemes not greatly exceeding the leaves, often short; spur usually somewhat globose at the tip; fruits often stout, commonly 10–15 mm. long; central United States........ 7. *C. micrantha* ssp. *micrantha*

EE. Normal-flowered racemes often greatly exceeding the leaves, elongated; spur not globose at the tip; fruits slender, 15–30 mm. long.

F. Stems usually weak and not strongly striate when dry; foliage green to glaucous; fruits 15–20 mm. long; south-central to southern United States........ 7a. *C. micrantha* ssp. *australis*

FF. Stems usually stout and strongly striate when dry; foliage glaucous; fruits 25–30 mm. long; coastal south Texas...... 7b. *C. micrantha* ssp. *texensis*

DD. Plants seldom bearing cleistogamous flowers (except in sp. 10); spurred petal mostly 14–18 mm. long; seeds about 2 mm. in diameter, essentially smooth to variously decorated under magnification.

E. Seeds distinctly muricate or muriculate under magnification; central Texas to southern Kansas.

F. Hood crestless or with a moderately well-developed crest; fruits 26–34 mm. long, usually abruptly acute; seeds distinctly muricate under magnification; central and western Texas........ 8. *C. curvisiliqua* ssp. *curvisiliqua*

FF. Hood with a well-developed crest; fruits 20–25 mm. long, gradually tapered; seeds muriculate under magnification; north Texas to southern Kansas........ 8a. *C. curvisiliqua* ssp. *grandibracteata*

EE. Seeds never muricate though sometimes muriculate at the margin under magnification.

F. Racemes usually surpassed by the leaves; hood sometimes crested; fruits spreading or pendent, usually 18–24 mm. long; seeds with no ring margin; northern United States to Alaska and southward in the Rocky Mountains to Mexico........ 9. *C. aurea* ssp. *aurea*

FF. Racemes usually surpassing the leaves (except in sp. 10); hood usually not crested; fruits erect, often incurved; seeds usually having a ring margin.

G. Cleistogamous flowers not present; fruits stout, incurved, usually 12–20 mm. long; southwestern United States and adjacent Mexico.......... 9a. *C. aurea* ssp. *occidentalis*

GG. Cleistogamous flowers present; fruits slender, not strongly incurved, 25–30 mm. long; mountains of eastern Mexico.......... 10. *C. pseudomicrantha*

With the exception of *C. sempervirens,* all the American species of Section EUCORYDALIS form a coherent group, with *C. flavula* and *C. crystallina* standing somewhat apart. *C. sempervirens,* although properly placed in this section, is quite distinctive in several ways, and conceivably could provide the basis for a subsection. Fedde (in Engler & Prantl, Nat. Pflanzenf. **17b**:129. 1936.) includes all of these species in his subsection EUCAPNOIDES of EUCORYDALIS.

4. C. SEMPERVIRENS (L.) Pers. Syn. Pl. **2**:269. 1807.

*Fumaria sempervirens* L. Sp. Pl. **2**:700. 1753.
*Neckeria sempervirens* Neck. Elem. Bot. **3**:60. 1790.
*Fumaria glauca* Curt. Bot. Mag. **5**: *t. 179.* 1792.
*Capnoides glauca* Moench, Meth. Pl. 52. 1794.
*Capnoides sempervirens* Borkh. in Roem. Arch. f. Bot. **1**$^2$:44. 1797.
*Corydalis glauca* Pursh, Fl. Am. Sept. **2**:463. 1816.
*Corydalis rosea* Eaton, Man. Bot. 79. 1817.
*Corydalis annua* Hoffmeg. ex Steudel, Nomen. Bot. ed. 2. **1**:423. 1841, as syn.
*Neckeria glauca* Millsp. Fl. W. Va. 327. 1892. (W. Va. Agr. Exp. Sta. Bull. 2),

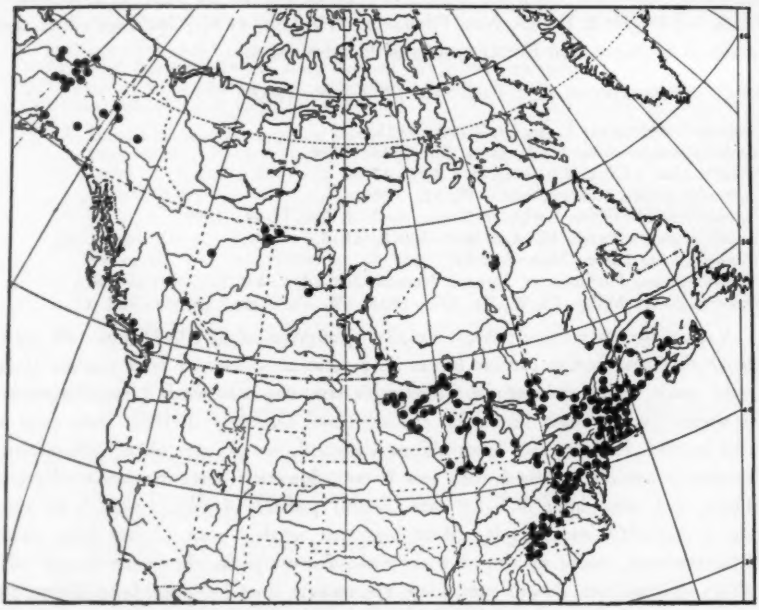
Very glaucous biennial; stems usually 1, approximately 30–80 cm. tall, much branched, erect; earlier cauline leaves long-petioled, crowded; later cauline leaves nearly sessile, much reduced; leaf blades pinnate, the basal with 5 main segments, the upper with 3 main segments, the segments ternately divided, then once or twice incised, the ultimate lobes oblong-elliptical, obtuse, apiculate; inflorescence a raceme or panicle, terminal, each axis 1- to 8-flowered; bracts narrowly elliptical, minute, 2–5 mm. long, 0.5–1.0 mm. broad; pedicels slender, erect, 5–20 mm. long at maturity, successively shorter upward; sepals 3 mm. or less long, ovate, short-attenuate, white or tinged with pink; flowers pink, the petals tipped with yellow; spurred petal 10–15 mm. long, the saccate spur 3–4 mm. long, blunt, the very short hood not crested, the wing margin minute but relatively broad, folded back upon the hood; spurless outer petal 10–13 mm. long; inner petals 9–12 mm. long, the slender claw 6–8 mm. long, occupying about two-thirds of the total length, the blade obovate, much broader near the apex, having a very high, angular, medial fold; stamen spur blunt, 1 mm. or less long, one-third the length of the petal spur; stigma slightly broader apically, with 4 papillary stigmatic surfaces; fruits erect, the slender body 25–50 (usually 30–35) mm. long, straight or somewhat curved, many-seeded; seeds about 1 mm. in diameter, black, shiny, turgid, distinctly decorated under magnification, the margin obtuse.

*C. sempervirens* is recognized easily by its erect habit, its divaricately branched stems, its pink and yellow flowers, its very slender, erect or spreading fruits, and numerous minute, decorated seeds. It has no close relatives in America.

This widely distributed species has no discernible geographical variants. Two

local variants, however, have been observed. Plants collected by Bartlett at Medford, Mass., have exceptionally stout, incurved fruits, and a collection made by Ehlers at Prentis Bay, Michigan, has unusually small flowers. It is doubtful if either of these variants is of nomenclatorial consequence.

In shallow, often dry soil, rock ledges, crevices, and talus, and on burned or otherwise disturbed areas, at elevations of about 500–5000 feet; northeastern Georgia to Maine and Newfoundland, thence westward to Montana and British Columbia and northwestward to Alaska. Flowers throughout the summer months from about May 15 to September 15; fruits from about June 1 to September 30.



Map 4. Distribution of *Corydalis sempervirens* (L.) Pers.

Georgia: Rabun County.
South Carolina: Pickens County.
North Carolina: Alexander, Buncombe, Burke, Caldwell, Forsythe, Haywood, Henderson, Jackson, Macon, Mitchell, Transylvania, Watauga, and Wilkes counties.
Tennessee: Carter County.
Kentucky: Bell and Harland counties.
Virginia: Augusta, Bedford, Carroll, Giles, Lee, Madison, Loudoun, Page, Pulaski, Rappahannock, Rockingham, Shenandoah, and Smythe counties; Shenandoah National Park.
West Virginia: Grant, Mineral, Monroe, Pocahontas, Preston, Raleigh, and Webster counties.
Maryland: Allegany, Frederick, and Garrett counties.
Pennsylvania: Adams, Bedford, Bucks, Elk, Fayette, Indiana, Lancaster, Luzerne, Lycoming, Monroe, Montgomery, Northampton, Perry, Philadelphia, Union, Westmoreland, and York counties.

New Jersey: Bergen, Essex, Hunterdon, Ocean, Passaic, Sussex, and Warren counties.

New York: Albany, Dutchess, Essex, Franklin, Greene, Herkimer, Jefferson, Nassau, Orange, Putnam, Rensselaer, St. Lawrence, Saratoga, Tompkins, Warren, Washington, and Westchester counties.

Connecticut: Fairfield, Hartford, Middlesex, New Haven, and New London counties.

Rhode Island: Providence County.

Massachusetts: Berkshire, Essex, Franklin, Hampden, Hampshire, Middlesex, Norfolk, Suffolk, and Worcester counties.

Vermont: Addison, Caledonia, Chittenden, Orange, Rutland, and Windham counties.

New Hampshire: Carroll, Cheshire, Coos, Grafton, and Hillsboro counties.

Maine: Aroostook, Cumberland, Franklin, Hancock, Knox, Lincoln, Oxford, Penobscot, Sagadahoc, Somerset, Washington, and York counties.

Ohio: Lake and Portage counties.

Indiana: Lake and Starke counties.

Illinois: Cook, LaSalle, and Ogle counties.

Michigan: Cheboygan, Crawford, Emmet, Ingham, Keweenaw, Leelanau, Mackinac, Marquette, Muskegon, and St. Clair counties.

Wisconsin: Adams, Ashland, Bayfield, Brown, Oneida, Polk, Sauk, Sawyer, Shawano, and Vilas counties.

Minnesota: Aitkin, Beltrami, Carlton, Cass, Chisago, Clearwater, Cook, Itasca, Lake, Millelacs, and St. Louis counties.

Montana: Flathead County; Glacier National Park.

Newfoundland: gravelly railroad embankments, Grand Falls, July 4, 1911, *Fernald & Wiegand 5455* (NY, G); sandy terraces, n. bank of river above the falls, Bishop's Falls, valley of Exploits River, July 28 & 29, 1911, *Fernald & Wiegand 5456* (G); dry woods, Buchan (?) Junction, July 13, 1930, *Jaussan* (G); railway, Gambo, July 14, 1893, *Wagborne 21* (UA).

Nova Scotia: digby co.—clearing at border of deciduous woods, Wentworth Lake, Sept. 4, 1921, *Fernald & Long 23866* (G). inverness co.—dripping cliffs, Big Intervale, July 17, 1941, *Roland 41416* (G). lunenburg co.—recently burned clearing w. of Bridgewater, Aug. 18, 1921, *Fernald & Long 23865* (G).

Prince Edward Island: prince co.—dry clearings, Alberton, July 11, 1912, *Fernald & St. John 7502* (WS, NY, G, US).

New Brunswick: kent co.—Bass River, June 10, 1869, *Fowler* (G).

Quebec: brome co.—Mt. Elephantis, Brome, July 30, 1902, *Pease 606* (G); dry mountain ledge, Bolton, July 25, 1926, *Knowlton* (G). chambly co.—St. Hubert: Tourbieres, environs de Montreal, June, 1913, *Victorin 206* (M, WS, US). charlevoix co.—vicinity of Cap à L'Aigle, July 27, 1905, *Macoun* (G). gaspé co.—alluvial woods, York River, July 29, 1905, *Williams, Collins & Fernald* (G). kamouraska co.—dry, quartzite hills, Ste. Anne, July 14, 1922, *Fernald & Pease 25088* (G). lake st. john dist.—carrière de granit, Roberval, July 20, 1921, *Victorin 15757* (G). megantic co.—dry, serpentine slopes and crests of Caribou Hill, Black Lake, Aug. 26, 1915, *Fernald & Jackson 12098* (G). nissisquoi co.—rocky places, Philipsburg, June 22, 1910, *Edmondson 4995* (G). montmagny co.—Grosse-Ile, l'estuaire du Saint-Laurent, July 31, 1935, *Victorin, Rolland-Germain, Rousseau & Meilleur 40082* (G). pontiac co.—Ile-des-Soeurs, Lake Timiscaming, June 26, 1918, *Victorin 8365* (US). richmond co.—dry ledge, Cleveland, July 30, 1923, *Chamberlain & Knowlton* (M, G). rimouski co.—dans un champ près du chemin du cap à l'Orignal, Aug. 19, 1927, *Rousseau 26971* (CIUC). terrebonne co.—sur les gneiss laurentiens, St. Jerome, July 4, 1930, *Victorin & Rolland-Germain 33122* (RM, G). two mts. co.—La Trappe, Oct. 9, 1926, *Louis-Marie* (G). co. uncertain—on rocks along Matamek River, n. shore, July 26, 1927, *Bowman 247* (G); Lac Kamatose, sur le ballast de la route, 101 milles au nord de Mont-Laurier, Aug. 23–25, 1941, *Victorin, Rolland-Germain & Dominique 260* (G).

Ontario: algona dist.—thin soil, e. ridge, Havilland Bay, 47° 00′ N., 84° 45′ W., Aug. 12, 1935, *Taylor, Hosie, Fitzpatrick, Losee & Leslie 1310* (US). carleton co.—Cascades, vicinity of Ottawa, July 31, 1920, *Victorin 10055* (WS). frontenac co.—

Battersea, June 13, 1898, *Edmondson 1106* (NY); Kingston, May 30, 1901, *Fowler* (G, US); Barriefield, June, 1897, *Boyd* (M). KENORA DIST.—Minaki, July 25, 1915, *Thompson 30* (M). LEEDS CO.—Jones Falls, June 7, 1895, *Fowler* (US). MUSKOKA DIST.—crevices of rocks, Lake Joseph, Muskoka, Aug. 20, 1881, *Burgess* (M); Lake Muskoka, Aug. 16–18, 1898, *Topping* (US). NIPISSING DIST.—common on sunny rocks, Twin Islands, Timagami region, July 24, 1926, *Anderson & Anderson 26039* (M, NY, G); Cache Lake, Algonquin Park, July 4, 1900, *Macoun* (US); open, grassy woods, Sturgeon Falls near Lake Nipissing, Aug. 14, 1937, *Nelson & Nelson 2395* (RM). PARRY SOUND DIST.—Island 74 in French River, July 5, 1939, *Dewey 1* (US); in soil pockets on granite ridge, s. side of French River Harbor, n. w. part of Parry Sound, Sept. 6, 1932, *Grassl 3766* (NY). RENFREW CO.—bluffs, Bonne Chere Mts., July 20, 1899, *Umbach* (US). THUNDER BAY DIST.—Mungo Park Point, Nipigon Lake, 1912, *Pulling* (G); crevice of altered lava, rocky knoll, flat e. of Schreiber, Aug. 21, 1937, *Hosie, Losee & Bannan 1412* (G); dry ledges, S. Slate Island, July 6, 1933, *Pease & Bean 23,549* (G); black loam along Amadis River, 1912, *Pulling* (G); diabase crevices, Shangoina Island, Sibley Tp., 48° 20′ N., 88° 50′ W., July 6, 1936, *Taylor, Losee & Bannan 505* (D). TIMISKAMING DIST.—Moose River Basin, 1903, *Bell* (G).

MANITOBA: SELKIRK DIST.—Elk Island, Lake Winnipeg, July 20, 1887, *Macoun* (NY). DIST. UNCERTAIN—Piguitonay (mile 214), route of Hudson Bay Railway, July 8, 1917, *Emerton* (G); Lake Winnipeg Valley, 1857, *Bourgeau* (G).

SASKATCHEWAN: north shore, Athabaska Lake, July 26, 1920, *Laing 174* (US); exposed rocky slopes, Charlot Pt., Lake Athabaska, about 59° 36′ N., 109° 13′ W., June 12, 1935, *Raup 6088* (G); in clay and sandy soil, Sulphide Lake (Lac la Ronge), Oct. 3, 1941, *Studer 4-16* (CIUC).

ALBERTA: ATHABASKA DIST.—Egg Lake, Athabaska Delta, July 18, 1920, *Harper 53* (US); Smith Landing, June 13, 1903, *Preble & Cary 13* (US); Granite Hill, Gov. Hay Camp district, Slave River, about 59° 31′ N., 11° 28′ W., Wood Buffalo Park, Mackenzie Basin, Aug. 14, 15, 1928, *Raup 2443-a* (G); short distance e. of Sand Point, n. shore of Lake Athabaska, about 58° 57′ N., 110° 42′ W., 700 ft. alt., Sept. 1, 1932, *Raup & Abbe 4531*. PEACE RIVER DIST.—Notikewin, Peace River region, roadside in poplar woods, 57° N., 118° W., July 12, 1931, *Moss 2255* (WS).

BRITISH COLUMBIA: CARIBOO DIST.—Hargreaves Ranch, 2900 ft. alt., Mt. Robson, Aug. 19–26, 1943, *Scamman 3272* (G, US); in brush on rocky slope, Campbell Island in Summit Lake, 31 mi. n. of Prince George, Aug. 1, 1941, *Weber 2600* (WS, M, NY, G, US). COAST DIST.—Bute Inlet, without date, *Anderson* (WS). KOOTENAY DIST.—Revelstoke, May 27, 1890, *Macoun* (US); deserted log road, Revelstoke, July 6, 1905, *Shaw 830* (NY, G, US). NEW WESTMINSTER DIST.—Cheak Kamis, June 25, 1920, ex herb. *Anderson* (WS); Mons, P. G. E. Railway, June 20, 1916, *Macoun* (NY, G).

YUKON: n. side of Moose Creek near Clark's Peak, 3500 ft. alt., Mayo District between Stewart and MacMillan Rivers, Aug. 7, 1939, *Bostock 60* (G); Klondyke, Aug. 23, 1898–1901, *MacLean* (UC, G); Moosehide Mt., Dawson, July 14, 1902, *Macoun* (NY); Bonanza Creek, Aug. 11, 1899, *Tarleton 178a* (NY); Dawson, July 17, 1898, *Williams* (NY).

ALASKA: edge of airfield, Franklin, Fortymile dist., July 16, 1941, *Anderson & Gasser 7320* (RM, G); dry ground, The Birches, 55 mi. below Tanana, on the Yukon River, July 8, 1902, *Brooks* (G); roadside near Knik, Oct., 1913, *Chaney 151* (M); Eagle to Valdes trail, June 30, 1902, *Collier 72* (US); headquarters, Mt. McKinley Nat. Park, June 28, 1932, *Dixon 45* (UC); Hot Springs on the Tanana River, July 28, 29, 1909, *Hitchcock* (US); Rampart, July 26, 1901, *Jones 67* (US); Mt. McKinley Nat. Park, summer, 1932, *Kaye 1501* (UC); Dall River Trail, 3 mi. above Dall City, Ft. Hamlin, Yukon River, to Bergman, Koyukuk River, June 29, 1901, *Mendenhall* (US); n. of superintendent's office, 3000 ft. alt., Mt. McKinley Nat. Park, July 23, 1928, *Mexia 2106* (M, UC, D, NY, G, US); exposed hillsides above spruce woods, e. side of Wonder Lake, near center of n. boundary of Mt. McKinley Nat. Park, Aug. 14, 1928, *Mexia 2240* (M, UC, D, NY, G, US); McKinley Park Station, July 31, 1922, *Murie* (US); rocky soil near Park Headquarters, Mt. McKinley Nat. Park, June 22, 1939, *Nelson & Nelson W-2151*

(RM); open woods just below Park Headquarters, Mt. McKinley Nat. Park, July 3, 1939, *Nelson & Nelson 3622* (RM, G); roadside near Park Headquarters, Mt. McKinley Nat. Park, July 16, 1939, *Nelson & Nelson 3833* (M, RM, IH, NY, G); Fairbanks, June, 1927, *Palmer 1769* (US); recent clearings and open woods, Goldstream Creek and Pedro Dome, 51 mi. n. of Fairbanks, 65° N., 147° 30′ W., 800–2000 ft. alt., June 13, 1926, *Porsild & Porsild 135* (G); open, forested bottom lands, Kokrines Mts., n. side of divide, towards Melozitna River, 65° 20′ N., 154° 30′ W., 800–4000 ft. alt., June 23–July 5, 1926, *Porsild & Porsild 739* (G); hill s. of Mitchell Creek, 3000 ft. alt., Copper River region, Aug. 6, 1902, *Poto 121* (US); Anchorage area, May 23, 1943, *York 4* (M); sandy hill-side near Palmer, July 5, 1943, *York Pa208* (M); Mt. McKinley Nat. Park, 63° 43′ N., 149° 15′ W., July 5–7, 1936, *Scamman 213* (G); Livengood, about 80 mi. n.-n.w. of Fairbanks, June 19–21, 1940, *Scamman 1735* (CIUC, G); Gens de Large (Chandler River) & Koyukuk rivers, 1899, *Schrader* (US).

5. C. FLAVULA (Raf.) DC. Prod. Syst. Nat. **1**:129. 1824.

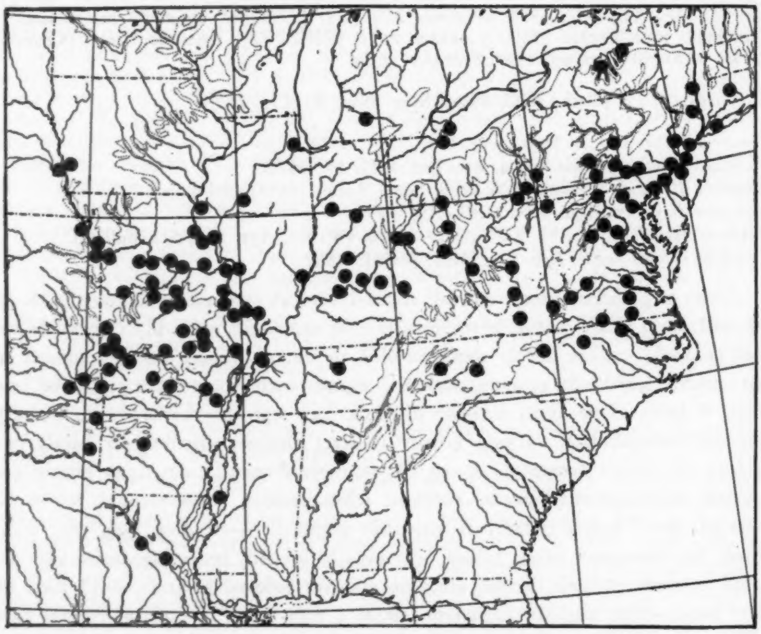
*Fumaria flavula* Raf. in Desv. Jour. Bot. **1**:224. 1808.
*Corydalis aurea* α *flavula* Wood, Am. Bot. & Fl. 34. 1870.
*Corydalis flavidula* Chapm. Fl. S. U. S. Suppl. **1**:604. 1883, sphalm.
*Capnodes flavulum* Ktze. Rev. Gen. **1**:14. 1891.
*Neckeria flavula* Millsp. Fl. W. Va. 327. 1892 (W. Va. Agr. Exp. Sta. Bull. 2).
*Corydalis Geyeri* Fedde, Rep. Spec. Nov. **10**:311. 1912.

Green or glaucous winter annual; stems 1–several, sympodial, commonly 15–30 cm. tall, erect while young, often prostrate or ascending when older; basal leaves long-petioled; cauline leaves short-petioled to almost sessile, hardly reduced in size upward; leaf blades pinnate, with 5–7 segments which are again pinnatifid into about 5 lobes, these again incised; ultimate leaf segments narrowly to broadly elliptical, subapiculate, varying greatly in size; racemes equalling or barely exceeding the leaves, commonly 6- to 10- or more flowered, sometimes poorly developed; cleistogamous-flowered racemes, when present, inconspicuous, 1- to 5-flowered; floral bracts broadly to narrowly elliptical, 6–12 mm. long, 3–7 mm. broad, the lowermost often foliose or variously incised, becoming entire and reduced upward; pedicels slender, erect at anthesis, reflexed in fruit, 6–15 mm. or more long; sepals scarious, fugacious, about 1 mm. long, lanceolate; flowers pale yellow, somewhat crowded; spurred petal 7–9 mm. long, the hood crested, the crest high, undulate or toothed, the wing margin well developed, also undulate or toothed, the incurved spur about 2 mm. long; spurless outer petal 6–8 mm. long, the crest and wing margin as in the spurred petal; clawed inner petals 5–7 mm. long, the claw 2–3 mm. long, the blade approximately twice as broad near the apex as at the distinctly lobed base; stamen spur less than 1 mm. long, less than one-half the length of the petal spur; stigma broader than high; fruits reflexed or variously disposed, 14–22 (often 18–20) mm. long, straight, essentially glabrous; seeds about 2 mm. in diameter, black, shiny, on magnification seen to be concentrically, submuricately decorated on the narrow, acute ring margin.

This species is easily distinguished by the small, crested flowers, the very short, incurved spur, and long, reflexed pedicels. Cleistogamous-flowered plants are col-

lected occasionally, and these often have much broader and larger ultimate leaf segments and weaker, more diffusely branched stems. Such plants can be determined accurately by fruit characters alone.

Moist, loose soil, wooded slopes and bottom lands, at elevations up to about 2000 feet; Connecticut and New York to North Carolina westward to northern Louisiana, eastern Oklahoma, Kansas and Nebraska. Flowers in early spring from about March 15 to May 15; fruits from about April 1 to June 1.



Map 5. Distribution of *Corydalis flavula* (Raf.) DC.

Connecticut: Middlesex County.

New York: Nassau, Onondaga, Rockland, Ulster, and Yates counties.

New Jersey: Camden, Hunterdon, Mercer, and Somerset counties.

Pennsylvania: Allegheny, Franklin, Huntingdon, Lancaster, Montgomery, Perry, Philadelphia, Snyder, Washington, and York counties.

Delaware: Newcastle County.

Maryland: Allegany, Baltimore, Carroll, Cecil, Hartford, Howard, Montgomery, and Prince Georges counties.

Virginia: Albemarle, Alexandria, Bedford, Botetourt, Buckingham, Dinwiddie, Fairfax, Fauquier, Greenesville, Henrico, Mecklenburg, Prince George, Prince William, Pulaski, Roanoke, Shenandoah, Stafford, Warren, and Wythe counties.

West Virginia: Berkeley, Cabell, Fayette, Monongalia, Ohio, and Raleigh counties.

North Carolina: Durham, Forsythe, Halifax, and Madison counties.

Kentucky: Fayette, Shelby, and Woodford counties.

Tennessee: Blount, Davidson, Knox, and Obion counties.

ALABAMA: Tuscaloosa County.
MISSISSIPPI: Sharkey County.
LOUISIANA: Natchitoches and Rapides parishes.
ONTARIO: Essex County, Point Pelee and Pelee Island.
MICHIGAN: Kalamazoo County.
OHIO: Clermont, Franklin, Hamilton, Ottawa, Ross, Scioto, and Warren counties.
INDIANA: Floyd, Lawrence, Marion, Montgomery, Orange, and Perry counties.
ILLINOIS: Hancock, Jackson, Mason, Pike, St. Clair, Union, Wabash, and Will counties.
MISSOURI: Barry, Boone, Butler, Callaway, Camden, Clay, Cooper, Franklin, Howell, Jackson, Jasper, Jefferson, Lawrence, McDonald, Madison, Maries, Marion, Montgomery, Morgan, Oregon, Ozark, Perry, Pettis, Phelps, Pulaski, St. Clair, St. Francois, Ste. Genevieve, St. Louis, Shannon, Texas, Warren, and Washington counties.
IOWA: Pottawattomie County.
NEBRASKA: Sarpy County.
KANSAS: Atchinson and Wyandotte counties.
OKLAHOMA: Adair, Cherokee, LeFlore, McCurtain, and Muskogee counties.
ARKANSAS: Carroll, Cross, Garland, Jackson, Searcy, Van Buren, and Washington counties.

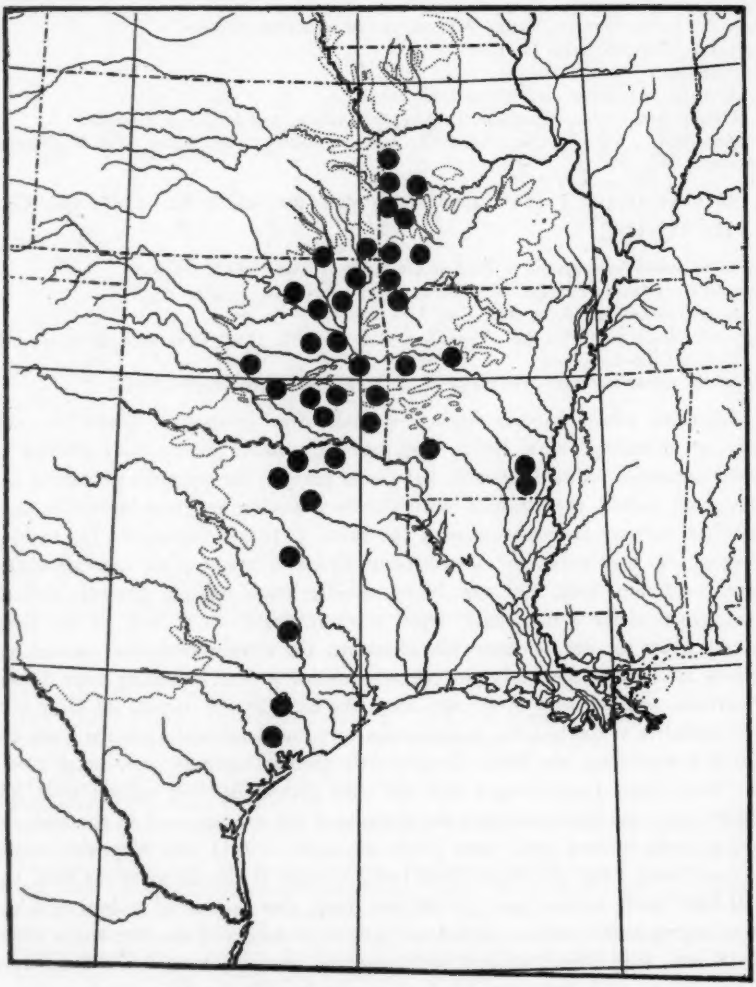
6. C. CRYSTALLINA Engelm. apud Gray, Man. Bot. ed. 5. 62. 1867; Bot. Gaz. **11**:189. 1886.

*Corydalis aurea β. ? crystallina* Torr. & Gray, Fl. N. Am. **1**:665. 1840.
*Corydalis crystallina* Engelm. ex Torr. & Gray, l. c. 1840, as syn.
*Capnodes crystallinum* Ktze. Rev. Gen. **1**:14. 1891.
*Capnoides Halei* Small, in Bull. Torr. Bot. Club **25**:137. 1898, as to most of Hale's collection from Louisiana.
*Corydallis crystallina* var. *strictissima* Fedde, Rep. Spec. Nov. **10**:479. 1912.

Glaucous winter annual; stems 1–several, often sympodial, 20–40 cm. tall, erect or ascending; basal leaves long-petioled; cauline leaves short-petioled to sessile, somewhat reduced upward; leaf blades pinnate, the segments pinnatifid and once again incised, the ultimate lobes broadly lanceolate to linear-lanceolate, subapiculate; primary racemes surpassing the leaves, 8- to 18- (ordinarily 12- to 15-) flowered, the later secondary racemes fewer-flowered; bracts ovate to ovate-acuminate, 5–12 mm. long, 3–6 mm. broad, usually much reduced upward; pedicels stout, erect, about 1 mm. long; sepals scarious, fugacious, 2 mm. or less long, broadly ovate to cordate, somewhat attenuate, the margin sometimes incised, especially at the base; flowers bright yellow, crowded at first, becoming more distant at anthesis; spurred petal 16–22 mm. long, the hood always crested, the crest very high, undulate or toothed, the wing margin very broad, reflexed upon the hood, the spur 6–8 mm. long, the blunt tip distinctly globose; spurless outer petal 12–14 mm. long, about 3 mm. longer than the inner petals, the wing margin wide, not reflexed upon the hood, enclosing the margins of the spurred petal in the bud, the crest as in the spurred petal; inner petals oblanceolate, 9–11 mm. long, the narrow claw 4–5 mm. long, the blade about twice as wide at the tip as at the base, the basal lobes small; stamen spur 3.5–5.0 mm. long, clavate, curved or bent near the apex; stigma about twice as broad as high; style long and slender; fruits erect, 14–18 mm. long, stout, straight or moderately incurved toward the floral axis, densely beset with transparent, clavate pustules which often break open at

maturity or, rarely, glabrate; seeds black, about 2 mm. in diameter, distinctly submuricately decorated under magnification, having no ring margin.

This species is distinguished from all other species of *Corydalis* by the peculiar type of pubescence of the fruit. The pustules sometimes appear ligulate when desiccated or, as is often the case, when they rupture at maturity. The crest and margins of the hood of the outer petals are more highly developed than in any other yellow-flowered species.



Map 6. Distribution of *Corydalis crystallina* Engelm.

*C. crystallina* var. *strictissima* is a habitat variant and of no systematic value. The type was collected by F. L. Harvey in "Orchards, grain fields, etc., Northwest Arkansas," and was distributed as Curtiss's North American Plants *125**. Fedde cites the collection but gives the number erroneously as *125a*. Too, he previously had described *C. micrantha* var. *diffusa*, a synonym of *C. micrantha* ssp. *australis*, on the basis of the true Curtiss's North American Plants distribution #*125a*, collected by Curtiss himself in Duval County, Florida.

Prairies, fields, open woods, and wasteland; southwestern Missouri to central Texas. Flowers in early spring from about April 1 to May 15; fruits from about April 15 to June 1.

MISSOURI: Bates, Benton, Cass, Greene, Henry, Jasper, Lawrence, McDonald, Newton, St. Clair, and Vernon counties.

ARKANSAS: Ashley, Benton, Carroll, Drew, Franklin, Nevada, Pope, Sebastian, and Washington counties.

KANSAS: Cherokee and Montgomery counties.

OKLAHOMA: Atoka, Cleveland, Craig, Haskell, Latimer, LeFlore, McCurtain, Mayes, Muskogee, Okmulgee, Osage, Pittsburg, Pontotoc, Pushmataha, Rogers, and Tulsa counties.

TEXAS: Brazos, Colorado, Denton, Fannin, Grayson, Kaufman, Lamar, Navarro, Tarrant, Van Zandt, and Victoria counties.

7. C. MICRANTHA (Engelm.) Gray ssp. **micrantha** G. B. Ownbey, stat. nov.

*Corydalis aurea* var. *micrantha* Engelm. apud Gray, Man. Bot. ed. 5. 62. 1867.
*Corydalis micrantha* Gray, in Bot. Gaz. **11**:189. 1886, in part.
*Neckeria micrantha* MacMillan, Metasp. Minn. Valley. 255. 1892.
*Capnoides micranthum* Britton, in Mem. Torr. Bot. Club **5**:166. 1894.
*Corydalis micrantha* var. *pachysiliquosa* Fedde, Rep. Spec. Nov. **10**:380. 1912.
*Corydalis monilifera* var. *ferruginifera* Fedde, l. c. **11**:498. 1913.

Glaucous or nearly green winter annual; stems 1–several, usually 15–25 cm. tall, erect or ascending, sparingly branched; basal leaves crowded, long-petioled; cauline leaves short-petioled to nearly sessile, gradually reduced upward; leaf blades pinnate, the 5–7 primary segments pinnatifid and again incised, the ultimate lobes oblong-elliptical or obovate, subapiculate; normal-flowered racemes usually present, slightly exceeding the leaves, 6- to 16-flowered, not surpassed by the fewer-flowered secondary racemes; cleistogamous-flowered racemes, when present, inconspicuous, 1- to 5-flowered; bracts elliptical, the lowermost 5–8 mm. long and 2–4 mm. broad, the upper much reduced, often minute on cleistogamous-flowered racemes; pedicels erect, the lower usually 2–4 mm. long, gradually decreasing in length upward; sepals scarious, fugacious, 1.5 mm. or less long, ovate, often undulate or toothed at the margin; flowers pale yellow, often somewhat crowded throughout anthesis; spurred petal 11–15, usually 12–14 mm. long, the hood crested, the crest low, undulate or rarely obsolescent, the wing margin well developed, the spur 4.5–6.0 mm. long, the apex distinctly globose; spurless outer petal 9–11 mm. long, semi-geniculate, the crest low; inner petals 7–9 mm. long, oblanceolate, the claw 3–4 mm. long, the blade twice as broad at the apex as at the obscurely lobed base; stamen spur 3–4 mm. long, about three-fifths the length of

the petal spur, straight or curved, sometimes clavate; stigma 2-lobed, rectangular, twice as wide as high; fruits erect, commonly 10–15 mm. long, rarely longer, often shorter in cleistogamous-flowered racemes, straight or moderately incurved; seeds about 1.5 mm. in diameter, black, shiny, turgid, concentrically but moderately decorated under magnification, obtuse at the border, with no ring margin.

The subspecies of *C. micrantha* are all characterized by very small seeds and can be distinguished from all other yellow-flowered species by them alone. Subspecies *micrantha* usually can be distinguished from ssp. *australis* by its less elongated racemes, generally smaller flowers, globose tipped spur and generally shorter, stouter fruits. The two subspecies intergrade in all of these characters, especially in southern Missouri and Oklahoma, but in most cases the disposition of a given specimen is not difficult. In southern Missouri a form is also found which is characterized by larger, more showy flowers, longer pedicels, and relatively short fruits. This large-flowered form has been confused by various authors with *C. aurea*. As flower size is not considered a good criterion for separation of the segregates of *C. micrantha*, this form seems better left with the typical subspecies.

A dwarf form of ssp. *micrantha* was collected by Reverchon at Columbia, Brazoria Co., Texas. This locality is far removed from the expected range of the subspecies and it seems likely that data on the label are mixed. Its presence there should be verified.

Although encountered occasionally in other species of *Corydalis* the cleistogamous condition reaches its highest development in *C. micrantha*. It occurs at random throughout the range of the species. A single plant may have only normal flowers, only cleistogamous flowers, or both cleistogamous and normal flowers. In the last instance, the cleistogamous flowers are produced only on the smaller, less well-developed secondary branches. Plants having only cleistogamous flowers are quite different in aspect, usually being much more profusely and delicately branched. The racemes are short, weak, and ordinarily have 1–5 small, undeveloped, self-fertilized flowers and ultimately the same number of fruits crowded near the apex. The disposition of such specimens is likely to prove difficult for one who is unfamiliar with this type of variation.

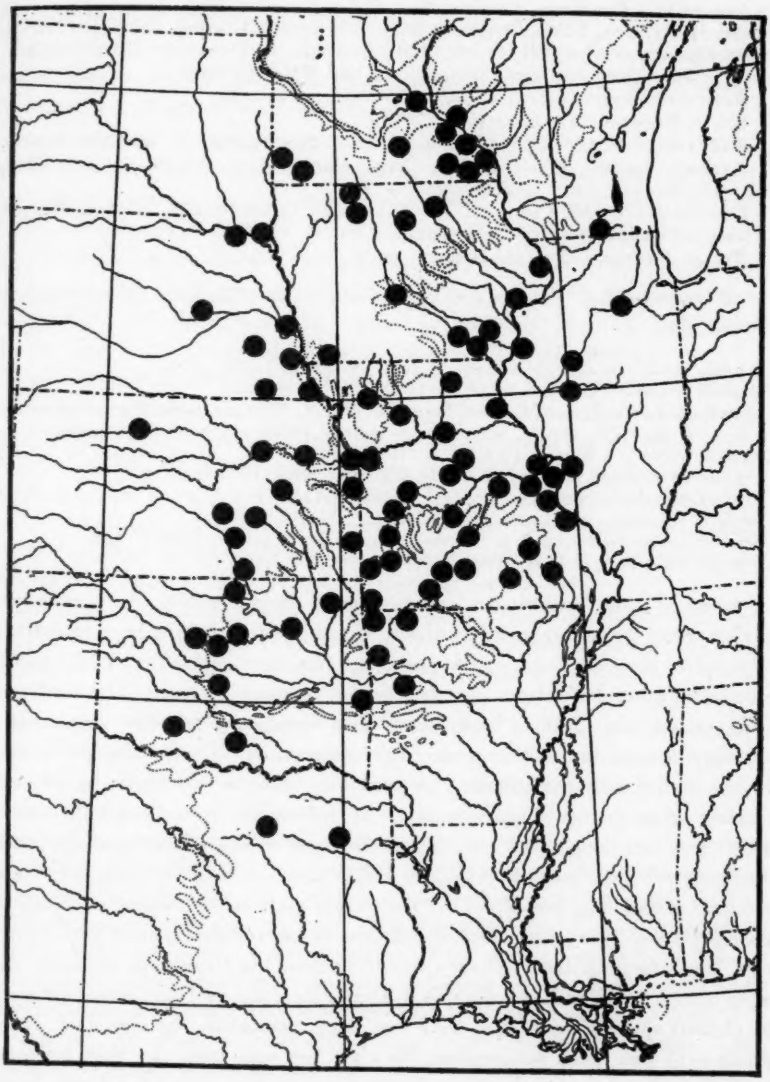
The conditions which institute cleistogamy are not entirely understood. It is notable, however, that plants growing in the shade or those which are crowded together so that they shade each other are predominantly cleistogamous. Also, age of the plant is of some significance, as the later racemes are often entirely cleistogamous on plants which at first produced only normal flowers.

Along bluffs, rocky hills, open woods, and river banks, often in disturbed soil; southern Minnesota to Illinois, Kansas, and northern Texas. Flowers in early spring from about April 1 to May 15; fruits from about April 15 to June 1.

MINNESOTA: Fillmore, Goodhue, Hennepin, Murray, Nobles, Olmsted, Pipestone, Steele, and Winona counties.

WISCONSIN: Pepin and Rock counties.

IOWA: Dickinson, Emmet, Floyd, Henry, Jackson, Muscatine, Page, Palo Alto, Polk, Van Buren, Wapello, and Wright counties.



Map 7. Distribution of *Corydalis micrantha* (Engelm.) Gray ssp. *micrantha* Ownbey.

ILLINOIS: Henderson, LaSalle, Menard, Peoria, and St. Clair counties.

MISSOURI: Adair, Boone, Camden, Cass, Cedar, Christian, Dade, Daviess, Gasconade, Greene, Henry, Iron, Jackson, Jasper, Jefferson, Lawrence, Livingston, McDonald, Marion, Miller, Moniteau, Phelps, Polk, Pulaski, Ralls, Randolph, St. Charles, St. Clair, Ste. Genevieve, St. Louis, Shannon, Stone, Texas, Wayne, and Webster counties.

ARKANSAS: Benton, Carroll, Logan, and Washington counties.

SOUTH DAKOTA: Clay County.

NEBRASKA: Cass, Cedar, Gage, Lancaster, Nance, Otoe, Richardson, and Sarpy counties.

KANSAS: Bourbon, Chase, Cowley, Geary, Harvey, Lyon, Miami, Osborne, Riley, Sedgwick, Shawnee, and Wyandotte counties.

OKLAHOMA: Carter, Comanche, Kay, Kingfisher, LeFlore, Logan, McClain, Murray, Oklahoma, Payne, Rogers, and Tulsa counties.

TEXAS: Brazoria, Dallas, and Upshur counties.

7a. C. MICRANTHA (Engelm.) Gray ssp. **australis** (Chapm.) G. B. Ownbey, stat. nov.

*Corydalis aurea* var. *australis* Chapm. Fl. S. U. S. Suppl. 1:604. 1883.
*Corydalis micrantha* Gray, in Bot. Gaz. **11**:189. 1886, in part.
*Capnoides Halei* Small, in Bull. Torr. Bot. Club **25**:137. 1898, as to the Curtiss collections from Jacksonville, Florida, but not as to most of Hale's specimens from Louisiana.
*Capnoides campestre* Britton, Man. ed. 2. 1065. 1905.
*Corydalis curvisiliqua* var. *tenerior* Fedde, Rep. Spec. Nov. **10**:365. 1912.
*Corydalis micrantha* var. *diffusa* Fedde, l. c. 380. 1912.
*Corydalis micrantha* var. *leptosiliqua* Fedde, l. c. **11**:497. 1913.
*Corydalis campestris* Buchholz & Palmer, in Trans. Acad. Sci. St. Louis **25**:115. 1926.
*Corydalis Halei* Fernald & Schubert, in Rhodora **48**:207. 1946.

Green or somewhat glaucous annual; stems 1–several, usually 20–40, occasionally up to 60 cm. tall, the earlier usually stouter, semi-erect, the later ascending; basal leaves crowded, long-petioled; cauline leaves short-petioled or nearly sessile, reduced upward; leaf blades pinnate, the 5–7 primary segments pinnatifid and again incised, the ultimate lobes longer than broad, approximately ovate, subapiculate; normal-flowered racemes usually present, much surpassing the leaves, 10- to 20-flowered, not surpassed by secondary racemes; cleistogamous-flowered racemes, when present, inconspicuous, 1- to 5-flowered; bracts elliptical, usually less than 8 mm. long and 4 mm. broad, the upper much reduced; pedicels erect, the lower 3–6 mm. long, decreasing in length upward; sepals scarious, fugacious, 1.5 mm. or less long, broadly ovate, the margin undulate or toothed especially at the base; flowers pale yellow, becoming distant during anthesis; spurred petal 12–14 mm. long, the hood nearly always crested, the crest low, regular or undulate, the wing margin well developed, the spur 4–6 mm. long, the tip blunt, never distinctly globose; spurless outer petal 9–11 mm. long, geniculate, the crest low; inner petals 8–10 mm. long, oblanceolate, the claw 3–4 mm. long, the blade twice as broad near the apex as at the obscurely lobed base; stamen spur 2.5–3.5 mm. long, about three-fifths the length of the petal spur, usually straight, sometimes bent near the tip, clavate; stigma 2-lobed, rectangular, twice as wide as high; fruits erect, 15–20, rarely 25 mm. long, slender, straight or moderately incurved; seeds

about 1.5 mm. in diameter, black, shiny, concentrically but moderately decorated under magnification, obtuse at the border, with no ring margin.

Subspecies *australis* is best distinguished by its elongate normal-flowered racemes, its short, saccate spur which is never clearly globose at the tip, its slender, erect fruits, and its minute, nearly smooth seeds.

The peculiarities of this plant were first recognized by Chapman who in 1883 published a short and accurate description of it in the first supplement to his 'Flora' under the name *Corydalis aurea* var. *australis*. In 1886 Gray (Bot. Gaz. **11**:189), in his study of *C. aurea* and its allies, concluded that Chapman's variety belonged with *C. micrantha* and reduced it to synonymy under that species. In conformance with Gray's treatment Chapman, then, also treated his variety as a synonym of *C. micrantha* in the third edition of his 'Flora' issued in 1897. The following year Small redescribed Chapman's plant as *Capnoides Halei*.

Small's description of *Capnoides Halei* was drawn on the joint basis of Hale's collection from Louisiana and Curtiss's collections from Florida. Hale's plants (s. n. in Herb. N. Y. Bot. Gard.), are all *C. crystallina* except for one small specimen which is referable to the subspecies described above. It is evident from the general aspect of the plants of *C. crystallina* that they are those referred to by Small in comparing the "new" species with *Capnoides curvisiliquum (Corydalis curvisiliqua)* when he distinguished it from that species by ". . . . its more slender habit, and especially by the more coarsely dissected leaf-blades."

Also cited by Small was *Curtiss 4515* from Jacksonville, Florida, and with the exception of the sentence quoted above, it is from these Florida specimens that the description is drawn. They, therefore, should be designated the authentic type if the species were maintained.

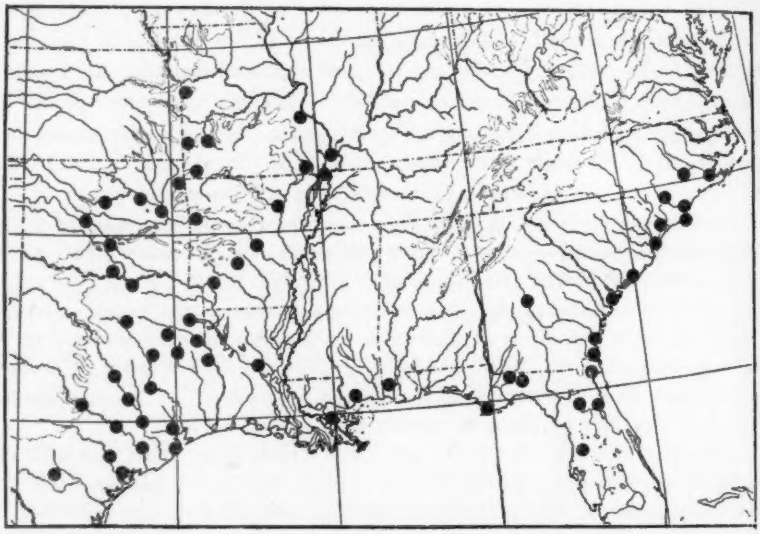
This entity has been the subject of a recent paper by Fernald and Schubert (Rhodora **48**:207. 1946) who, recognizing its distinctness, have revived Small's name, and transferred it to *Corydalis*. I do not believe, however, that the differences between this and ssp. *micrantha* are of specific level, and am therefore taking up Chapman's earlier varietal name *australis* in its new rank of subspecies. In support of this view it may be mentioned that seeds of ssp. *micrantha* and ssp. *australis* are identical in size and decoration of the testa, that the flowers are similar in that both have a low crest, and that the geographical distrubution of the two subspecies taken as a whole is not unnatural. Even greater variability in habit, together with similar minor morphological variability of the floral organs and fruits, is found in other species of *Corydalis* such as *C. aurea* and *C. Caseana*.

Plants of ssp. *australis* from coastal North Carolina, South Carolina, and Georgia are appreciably smaller and more strict in habit than those from other parts of the range of the subspecies. The flowers also are noticeably smaller, the hood is not crested, and the fruits are very slender and often moniliform.

The center of diversity of this subspecies is eastern Oklahoma and southeastern Missouri, and plants intermediate between this subspecies and ssp. *micrantha* and

*C. curvisiliqua* are not uncommonly collected in this area. The disposition of a given specimen, however, ordinarily is not difficult.

In disturbed, often sandy soil, abandoned fields and waste areas, along roadsides, and in open woods; from southern Missouri and eastern Kansas to Texas, Florida, and North Carolina. Flowers in early spring, about February 15 to April 30; fruits from about March 1 to May 15.



Map 8. Distribution of *Corydalis micrantha* (Engelm.) Gray ssp. *australis* (Chapm.) Ownbey.

North Carolina: Bladen, Brunswick, Craven, Jones, Lenoir, and New Hanover counties.

South Carolina: Beaufort, Charleston, Georgetown, and Horry counties.

Georgia: Camden, Glynn, and Pulaski counties.

Florida: Alachua, Duval, Franklin, Hernando, Leon, Marion, Nassau, Putnam, and St. John counties.

Alabama: Mobile County.

Mississippi: Harrison County.

Louisiana: Jefferson, Natchitoches, Orleans, and Rapides parishes.

Texas: Anderson, Austin, Bastrop, Bell, Brazos, Burleson, Caldwell, Clennan, Dallas, DeWitt, Frio, Galveston, Gonzales, Grayson, Gregg, Harris, Henderson, Jackson, Kaufman, McLennan, Nueces, Rusk, San Augustine, Smith, Tarrant, Travis, Upshur, Victoria, Waller, Washington, and Wharton counties.

Oklahoma: Carter, Cleveland, Creek, Logan, Murray, Muskogee, Oklahoma, Payne, and Pottawatomie counties.

Arkansas: Benton, Crawford, Hempstead, Hot Spring, Jackson, and Pulaski counties.

Missouri: Barry, Carter, Cedar, Dunklin, Jackson, Jefferson, Madison, Mississippi, St. Clair, Scott, and Vernon counties.

Kansas: Miami County.

7b. CORYDALIS MICRANTHA (Engelm.) Gray ssp. **texensis** G. B. Ownbey, ssp. nov.

Herbae annuae glaucae; caulibus 20–45 cm. longis saepe crassis post exsiccationem valde striatis; foliorum laminis pinnatis, segmentis primariis pinnatifidis incisis ultimis oblongo-acutis subapiculatis; racemis saepe crassis folia superantibus, bracteis ovato-attenuatis margine denticulatis infimis ca. 5 mm. longis 2 mm. latis superioribus aliquid minoribus; floribus flavis primo congestis in anthesim remotioribus, pedicellis erectis patulisve 2–4 mm. longis, sepalis fugaceis ca. 1.5 mm. longis ovato-attenuatis, petalo calcarato valde arcuato 12–15 mm. longo carinae cristo satis humili undulato margine bene manifesto supra cristum inflexo calcare obtuso haud globoso, petalo ecalcarato exteriori ca. 10 mm. longo margine haud reflexo duobus interioribus 8–10 mm. longis oblanceolatis ungui 3–4 mm. longo, lamina apice quam basi multo latiori, calcare staminali ca. 2 mm. longo clavato, stigmate 2-lobato ca. bis longiori latiori; fructibus erectis vel incurvatis gracilibus 25–30 mm. longis; seminibus ca. 1.5 mm. diam. sub lente aliquid ornatis margine obtuso.

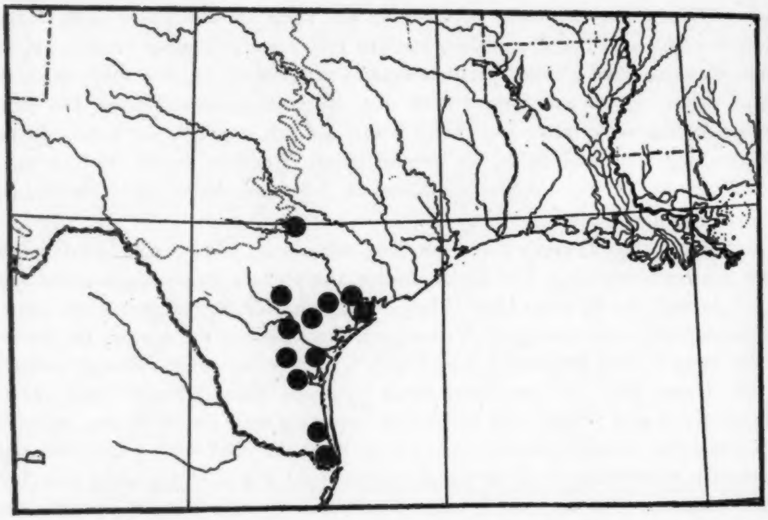
Glaucous annual; stems 20–45 cm. long, often stout and strongly striate when dry, prostrate-ascending; leaf blades pinnate, the primary segments pinnatifid and again incised, the ultimate lobes oblong-acute, subapiculate; racemes often stout, surpassing the leaves; bracts ovate-attenuate, denticulate at the margin, the lowermost about 5 mm. long and 2 mm. broad, the upper somewhat reduced; pedicels erect or spreading, 2–4 mm. long; sepals fugacious, about 1.5 mm. long, ovate-attenuate; flowers yellow, crowded at first, becoming more distant during anthesis; spurred petal strongly arcuate, 12–15 mm. long, the hood with a low undulate crest, the wing margin well developed, reflexed upon the hood, the blunt spur 5–7 mm. long, not globose; spurless outer petal about 10 mm. long, the margin not reflexed; inner petals 8–10 mm. long, oblanceolate, the claw 3–4 mm. long, the blade much broader at the apex than at the base; stamen spur about 2 mm. long, clavate; stigma 2-lobed, twice as broad as high; fruits erect or incurved, slender, 25–30 mm. long; seeds about 1.5 mm. in diameter, moderately decorated under magnification, obtuse at the border, with no ring margin.

This well-defined subspecies is endemic to the coastal plain of southern Texas. It is most closely comparable to ssp. *australis*, but is easily distinguished by its longer fruits and more strongly arcuate spurred petal. In habit and foliage it is very similar to C. *curvisiliqua* ssp. *curvisiliqua* with which it is often confused. It can be distinguished from the latter by its non-muricate seeds and shorter spur which is not globose at the tip.

Moist, often sandy soil, open ground of alluvial plains and uplands; south coastal Texas. Flowers in early spring from about February 20 to March 20; fruits from about March 1 to April 10.

TEXAS: ATASCOSA CO.—moist, alluvial ground, Campbelton, March 10, 1917, *Palmer 11239* (M, G, US). BEE CO.—Beeville, March 30, 1932, *Jones 29365* (M, TYPE). CALHOUN CO.—Bahia del Espiritu-Santo, ex herb. *Berlandier 548, 1799, 1933* (G). CAMERON

co.—Palm Grove, March 3, 1940, *Parks 1429* (M). GOLIAD CO.—Goliad, Feb., 1927, *Williams 11* (UT). JIM WELLS CO.—sandy loam, about 600 ft. alt., Romarsid Ranch, March 18, 1943, *Freeborn 338* (UT). KENDALL CO.—Edge Falls, March 26, 1938, *Parks 29500* (G). KLEBERG CO.—Riviera, Feb. 22, 1930, *Harrison* (US). LIVE OAK CO.—sandy upland, 41 mi. n. of Alice, March 1, 1944, *Painter & Barkley 14461* (UT). NUECES CO.—Corpus Christi, May, 1913, *Orcutt 5829* (M); Robstown, March 26, 1920, *High 91* (M). VICTORIA CO.—Victoria, April 6, 1900, *Eggert* (M); sandy, open ground, Victoria, March 4, 1916, *Palmer 9064* (M, D, US); Victoria-Goliad, March 29, 1930, *Tharp* (UT). WILLACY CO.—in open ground, sandy situations, March 21, 1937, *Runyon 1618*.



Map 9. Distribution of *Corydalis micrantha* (Engelm.) Gray ssp. *texensis* Ownbey.

8. C. CURVISILIQUA Engelm. ssp. **curvisiliqua** G. B. Ownbey, stat. nov.

*Corydalis aurea* var. *curvisiliqua* Gray, in Proc. Acad. Phila. **1863**:57. 1864, nom. nud.
*Corydalis curvisiliqua* Engelm. ex Gray, l. c. 1864, nom. nud. in synon.; apud Gray, Man. Bot. ed. 5: 62. 1867; Bot. Gaz. **11**:188. 1886.
*Capnoides curvisiliqua* Ktze. Rev. Gen. **1**:14. 1891.
*Neckeria curvisiliqua* Rydb. in Univ. Nebr. Bot. Surv. Nebr. **3**:24. 1894.

Glaucous winter annual or perhaps biennial; stems 1–several, the primary often erect, the 1–several secondary ascending, 10–40 cm. long, often somewhat branched; basal leaves long-petioled; cauline leaves short-petioled, reduced in size; leaf blades pinnate, the pinnae twice pinnatifid, rarely again incised, the ultimate segments oblong, obtuse or rounded; peduncles usually surpassing the leaves, the primary 6- to 18-, usually about 12-flowered; the secondary fewer-flowered; bracts ovate, 10 mm. or less long, 6 mm. or less wide, the lowest sometimes foliose, much reduced upward; pedicels stout, spreading, 2–3 mm. long; sepals scarious,

broadly ovate to ovate-attenuate, often more or less toothed or undulate at the margin, about 1 mm. long; flowers bright yellow, often strongly arcuate, crowded on the raceme at first, becoming more distant during anthesis; spurred petal 16–18 mm. long, with a very broad wing margin, the crest absent to well developed and undulate or toothed, the spur 7–9 mm. long, often somewhat globose at the blunt tip; spurless outer petal 12–15 mm. long, geniculate, about 3 mm. longer than the inner petals, the crest similar to that of the spurred petal; inner petals oblanceolate, 9–11 mm. long, the slender claws nearly half the total length; stamen spur clavate, bent near the apex, 4–6 mm. long; stigma 2-lobed, twice as broad as high; style slender; fruits slender, erect, moderately to strongly arcuate or incurved toward the floral axis, usually 26–34 mm. long; seeds about 2 mm. in diameter, black, muricate, with essentially no ring margin at maturity.

Subspecies *curvisiliqua* is most easily recognized by its extremely long, erect, incurved fruits, and its seeds which are distinctly muricate under magnification. The latter character is approached nowhere else in the genus, and, indeed, is the strongest character upon which the species is based. The tetragonal character of the fruits mentioned by Gray (Bot. Gaz. **11**:189. 1886), although perhaps more pronounced here, especially in fresh material, is by no means unique.

Floral characters which are of value in recognizing this subspecies are the well-developed wing margins of the outer petals, the much-reduced, claw-like basal portion of the unspurred outer petal, and the well-developed spur which is about one-half the total length of the spurred petal. The degree to which the crest is developed is extremely variable; material from the type locality usually has no apparent crest. Some plants, however, have a moderately well developed crest. This diversity is general throughout the range of the subspecies.

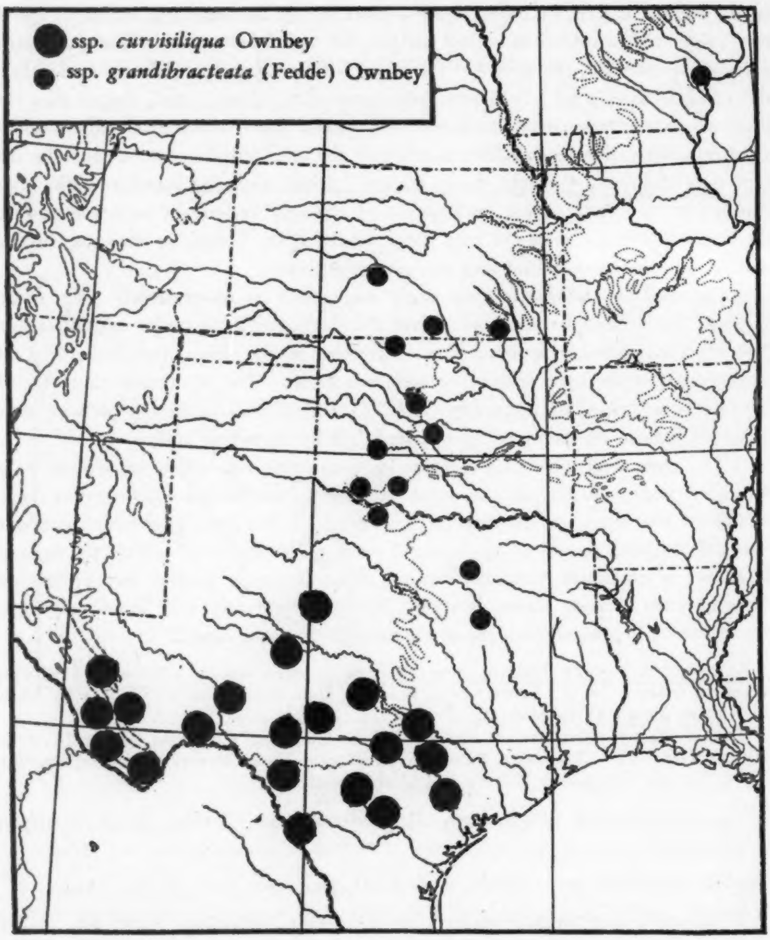
Disturbed soil, sandy bottoms, abandoned fields, open woods, hillsides, and valleys; central to western Texas. Flowers in early spring from about March 1 to May 1; fruits from about March 15 to May 15.

TEXAS: Bexar, Brewster, Caldwell, Comal, Crockett, Culberson, Edwards, Frio, Gillespie, Hays, Irion, Jeff Davis, Karnes, Kerr, Kinney, Llano, Maverick, Medina, Presidio, Taylor, Terrell, Tom Green, Travis, and Uvalde counties.

8a. C. CURVISILIQUA Engelm. ssp. **grandibracteata** (Fedde) G. B. Ownbey, stat. nov.

*Corydalis curvisiliqua* var. *grandibracteata* Fedde, Rep. Spec. Nov. **11**:291. 1912.

Glaucous winter annual; stems 1–several, stout, ascending, commonly 20–30 cm. long; basal leaves numerous, moderately long-petioled; cauline leaves somewhat reduced, shorter-petioled; leaf blades pinnate, the primary segments pinnatifid and usually again incised, the ultimate segments elliptical to obovate; peduncles stout, surpassing the leaves; bracts conspicuous, usually ovate-acuminate, the lowermost usually 10–15 mm. long and 4–6 mm. wide, somewhat reduced upward; pedicels spreading, usually 2–3 mm. long; sepals ovate, variously toothed; flowers bright yellow; spurred petal 15–18 mm. long, having a well-developed wing margin, the hood crested, the crest conspicuous, regular or undulate, the stout spur 7–9 mm.




Map 10. Distribution of *Corydalis curvisiliqua* Engelm.

long, somewhat globose at the tip; spurless outer petal 12–15 mm. long, geniculate, the basal portion slender, claw-like, the crest similar to that of the spurred petal; inner petals oblanceolate, 9–11 mm. long, the claw slender, 4–5 mm. long; stamen spur about two-thirds the length of the petal spur; stigma twice as broad as high; style slender; fruits slender, erect, incurved toward the floral axis, 20–25 mm. long, gradually tapered apically; seeds about 2 mm. in diameter, black, having a narrow ring margin, distinctly muriculate under magnification.

This subspecies is best distinguished by its slender, lanceolate, erect, incurved fruits, its relatively large flowers, the usually highly developed crest and wing margin, and the large ovate floral bracts. The muriculate character of the seeds, so striking in ssp. *curvisiliqua*, is here reduced nearly to the condition found in *C. aurea* ssp. *occidentalis*. Hybridization between the two and with *C. micrantha* ssp. *australis* may account for the anomalous nature of many specimens. However, because of the greatest agreement in floral morphology with *C. curvisiliqua* and because its range is a northward extension of that species I believe that it is properly placed here.

The isolated occurrence of ssp. *grandibracteata* in Muscatine Co., Iowa, perhaps is best explained by a chance introduction of seeds.

Usually in sandy soil, open ground, alluvial plains, roadsides, prairies, and slopes; southern Kansas to northern Texas; eastern Iowa. Flowers from about April 15 to May 15; fruits from about May 1 to May 30.

IOWA: Muscatine County.

KANSAS: Chautauqua, Stafford, and Sumner counties.

OKLAHOMA: Alfalfa, Caddo, Canadian, Cleveland, Comanche, Grady, Kingfisher, Kiowa, Logan, McClain, Oklahoma, and Stephens counties.

TEXAS: Archer, Clay, Collin, Dallas, and Navarro counties.

9. C. AUREA Willd. ssp. **aurea** G. B. Ownbey, stat. nov.

*Corydalis aurea* Willd. Enum. Hort. Berol. **2**:740. 1809.
*Fumaria aurea* Muhl. ex Willd. l. c. 1809, as syn.
*Fumaria aurea* Ker, Bot. Reg. **1**:*t. 66*. 1815.
*Odoptera aurea* Raf. Cat. 15. 1824.
*Corydalis montana* Engelm. ex Gray, in Mem. Am. Acad. **4**:6. 1849, nom. nud. in synon.
*Corydalis aurea* var. *typica* Regel, in Mem. Acad. St. Petersb. **4**$^4$:19. 1861 (Tent. Fl. Ussuri. 19. 1861); Bull. Soc. Mosc. **34**$^3$:145. 1861.
*Corydalis aurea* var. *parviflora* Regel, in Bull. Soc. Mosc. **34**$^3$:146. 1861.
*Corydalis aurea* β. *macrantha* Wood, Am. Bot. & Fl. 34. 1870.
*Capnodes aureum* Ktze. Rev. Gen. **1**:14. 1891.
*Neckeria aurea* Millsp. Fl. W. Va. 327. 1892 (W. Va. Agr. Exp. Sta. Bull. 2).
*Corydalis Wetherillii* Eastw. in Bull. Torr. Bot. Club **29**:524. 1902.
*Corydalis wyomingensis* Fedde, Rep. Spec. Nov. **10**:312. 1912.
*Corydalis tortisiliqua* Fedde, l. c. 313. 1912.
*Corydalis Gooddingii* Fedde, l. c. 1912.
*Corydalis hypecoiformis* Fedde, l. c. 314. 1912.
*Corydalis Engelmannii* Fedde, l. c. 365. 1912.
*Corydalis aurea* var. *robusta* Fedde, l. c. 379. 1912.
*Corydalis monilifera* Fedde, l. c. 417. 1912.
*Corydalis washingtoniana* Fedde, l. c. 419. 1912.
*Corydalis macrorrhiza* Fedde, l. c. 479. 1912.
*Corydalis Albertae* Fedde, l. c. **11**:196. 1912.
*Corydalis Jonesii* Fedde, l. c. 1912.

*Corydalis oregana* Fedde, l. c. 290. 1912.
*Corydalis densicoma* Fedde, l. c. 291. 1912.
*Capnoides Wetherillii* Heller, in Muhlenbergia 7:123. 1912.
*Capnoides euchlamydeum* Woot. & Standl. in Contr. U. S. Nat. Herb. 16:122. 1913.
*Corydalis tortisiliqua* var. *longibracteata* Fedde, l. c. 11:497. 1913.
*Corydalis Engelmannii* var. *exaltata* Fedde, l. c. 1913.
*Corydalis isopyroides* Fedde, l. c. 498. 1913.
*Corydalis isopyroides* var. *Mearnsii* Fedde, l. c. 12:37. 1913.
*Corydalis wyomingensis* var. *lativaginata* Fedde, l. c. 38. 1913.
*Capnoides Engelmannii* Cockerell, in Univ. Colo. Stud. 11:216. 1915.
*Capnoides macrorrhiza* Cockerell, l. c. 1915.
*Corydalis euchlamydea* Fedde, l. c. 18:32. 1922.

Glaucous winter annual or biennial from a more or less branched caudex; stems sympodial, prostrate-ascending, 10–50, usually 20–35 cm. long; basal leaves long-petioled; cauline leaves barely reduced in size upward, also usually long-petioled; leaf blades pinnate, with 5–7 pinnae, these pinnatifid into about 5 segments which are again incised; ultimate leaf segments broadly to narrowly elliptical, 1.5–several times as long as broad, greatly variable in gross size, subapiculate; peduncles short, terminal; racemes shorter than to barely exceeding the leaves, the primary 10- to 30-, usually 10- to 20-flowered, the secondary 4- to 12-flowered; bracts elliptical to linear, the lowest 4–10 mm. long and 1–2 mm. broad, rarely larger, often denticulate at the apex, much reduced upward; pedicels erect when young, generally reflexed or recurved in fruit, the lowermost 5–10 mm. long; sepals scarious, fugacious, broadly ovate or ovate-attenuate, irregularly toothed, 1–3 mm. long; flowers pale to bright yellow; spurred petal 13–16 mm. long, the hood usually not crested, the crest when present low and incised, the wing margin moderately to well developed, the spur straight or slightly incurved, 4–5 mm. long, the tip somewhat globose; spurless outer petal 9–11 mm. long, the hood and crest as in the spurred petal; inner petals 8–10 mm. long, the claw 3.5–4.5 mm. long, the blade somewhat broader and more distinctly winged distally; stamen spur 2–3 mm. long; stigma about twice as broad as high; fruits commonly 18–24, rarely up to 30 mm. long, usually slender, often erect when young, generally pendent at maturity, straight to moderately arcuate, often moniliform, the valves often torulose when dry; seeds nearly 2 mm. in diameter, black, shiny, turgid, obscurely decorated to nearly smooth under magnification, broadly acute at the edge, with no ring margin.

This subspecies is best distinguished on the basis of the generally weak racemes and slender, pendent or spreading fruits. The racemes ordinarily do not exceed the leaves except in early stages of growth. It intergrades at times with ssp. *occidentalis*, but in general can be distinguished without difficulty when the plant is in fruiting condition.

Contingent upon the broad view of the subspecies adopted here it has been necessary to reduce to synonymy a large number of specific and varietal epithets proposed by Fedde. For the most part, they are founded upon minor variant forms which are by no means mutually exclusive. A brief discussion of the proposed

biological basis for the type of variability found in *C. aurea* is given in the introductory material to this paper.

*Corydalis aurea* ssp. *aurea* is of north temperate and subarctic distribution. In the northern part of its range it is found at low elevations, but in the southern part it is confined largely to mountainous districts, and may grow at elevations of 11,000 feet or more. Consequent to its wide range and adaptation to a diversity of habitats, this subspecies has become quite polymorphic. It seems probable that a good deal of minor genetic differentiation has taken place in each of the isolated mountain ranges of the Southwest. Ultimately the many forms thus produced may be of nomenclatorial rank. At present their nomenclatorial recognition can add nothing to an understanding of the group.

Among the many recognizable variants which in my opinion are not nomenclatorially important the following are mentioned briefly:

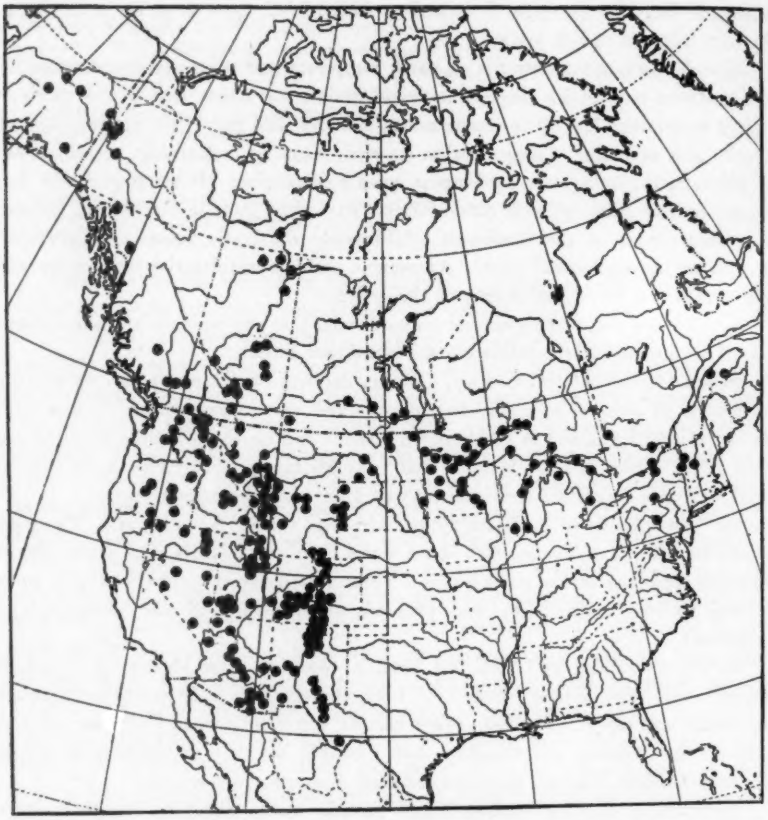
Plants from Rimouski County, Quebec, described as *C. aurea* var. *robusta* by Fedde, are of interest primarily because of their very foliose stems. Plants with similar foliage are found in southeastern Canada and northern United States as far west as the shores of Lake Superior and Lake Michigan. Fruit characters emphasized by Fedde do not set these plants apart from the subspecies proper.

At low elevations in Washington, Oregon, Idaho, Nevada, and Wyoming plants sometimes are found with stout stems, semi-erect fruits, and short, obtuse ultimate segments of the basal leaves. These are all better placed with ssp. *aurea* because of the unreliability and probable superficiality of the distinguishing characters.

In the mountains of Otero and Lincoln counties, New Mexico, is a variant having very large, foliose bracts. In fruit characters it is intermediate between ssp. *aurea* and ssp. *occidentalis*. This variant was described as *Capnoides euchlamydeum* by Wooton and Standley, but I cannot see that the differences are in any way essential, and am therefore reducing the name to synonymy.

Particularly striking variant forms having weak, diffusely branched, leafy stems, weak, 1- to 4-flowered racemes, and very broad, incompletely divided ultimate leaf segments occur sporadically throughout the Southwest. Among many localities where plants of this description are found may be mentioned especially Crandall Canyon, Carbon County, Utah, the Charleston Mts., Clark County, Nevada, the Grand Canyon National Park, Arizona, the Santa Catalina and Chiricahua Mts., Arizona, the Black Range, Grant and Sierra counties, New Mexico, the Guadalupe Mts., Culberson County, Texas, and the Davis Mts., Jeff Davis County, Texas. The tendency for plants of this sort to be produced, therefore, is widespread. Viewed separately they often appear significantly different, but against the background of the subspecies proper their significance fades.

Although the outer petals of ssp. *aurea* ordinarily are not crested, an occasional exception to this generalization is met with in northern and western United States. The fact that the presence of a crest apparently is not tied up with any constant morphological difference, together with its erratic occurrence, leads me to believe that it does not warrant serious consideration.



Map 11. Distribution of *Corydalis aurea* Willd. ssp. *aurea* Ownbey.

Loose, open, often gravelly soil, lake shores, talus slopes, ledges, rocky hillsides and creek bottoms, gravel pits, road cuts, and burned-over areas; northeastern United States, northward and westward to Quebec, the Dakotas, Mackenzie, and Alaska, southward in the Rocky Mountains to Arizona, New Mexico and western Texas, at elevations of a few hundred feet in northern United States and Canada to over 11,000 feet in the Colorado Rockies. Flowers throughout the summer months, from about May 1 to August 30; fruits from about May 15 to September 15.

Pennsylvania: Snyder County.

New York: Essex, Jefferson, and Tompkins counties.

Vermont: Addinson, Chittenden, Rutland, and Windsor counties.

New Hampshire: Grafton County.

Illinois: Cook and Winnebago counties.

Michigan: Alpena, Keewenaw, Mackinac, Montmorency, Oscoda, and Schoolcraft counties.

Wisconsin: Brown and Door counties.

Minnesota: Aitkin, Becker, Beltrami, Carlton, Cass, Chisago, Clearwater, Cook,

Crow Wing, Dakota, Goodhue, Hennepin, Hubbard, Lake, Meeker, Ottertail, Polk, Pope, Ramsey, Renville, St. Louis, Todd, Wabasha, and Winona counties.

SOUTH DAKOTA: Brookings, Custer, Fall River, Harding, Lawrence, Meade, and Pennington counties.

NORTH DAKOTA: Benson, McLean, Morton, Pembina, and Rolette counties.

MONTANA: Carbon, Cascade, Chouteau, Deerlodge, Flathead, Gallatin, Jefferson, Lewis & Clark, Meagher, Missoula, Park, Powell, and Ravalli counties; Glacier National Park.

WYOMING: Albany, Big Horn, Crook, Fremont, Johnson, Lincoln, Park, Sheridan, Sublette, Teton, and Uinta counties; Yellowstone National Park.

COLORADO: Boulder, Chaffee, Clear Creek, Conejos, Custer, El Paso, Fremont, Gilpin, Grand, Gunnison, Hinsdale, Jefferson, Lake, La Plata, Larimer, Mineral, Montezuma, Montrose, Ouray, Park, Pueblo, Rio Grande, Saguache, San Juan, Summit, Teller, and Weld counties; Rocky Mountain National Park.

NEW MEXICO: Bernalillo, Catron, Colfax, Dona Ana, Eddy, Grant, Lincoln, Luna, Mora, Otero, Rio Arriba, Sandoval, San Miguel, Santa Fe, Sierra, Socorro, and Taos counties.

TEXAS: Brewster, Culberson, and Jeff Davis counties.

ARIZONA: Apache, Cochise, Coconino, Gila, Graham, Mohave, Pima, and Yavapai counties; Grand Canyon National Park.

UTAH: Beaver, Cache, Carbon, Daggett, Duchesne, Garfield, Iron, Salt Lake, San Juan, San Pete, Summit, Uintah, Utah, and Wasatch counties.

NEVADA: Clark, Elko, Esmeralda, Humboldt, Lincoln, Nye, and White Pine counties.

CALIFORNIA: Modoc County.

IDAHO: Bannock, Blaine, Bonner, Clark, Custer, Fremont, Kootenai, and Owyhee counties.

OREGON: Crook, Grant, Harney, Lake, and Wallowa counties.

WASHINGTON: Chelan, Douglas, Ferry, Kittitas, Okanogan, Pend Oreille, Spokane, Stevens, and Whitman counties.

QUEBEC: BONAVENTURE CO.—Restigouche River, Matapedia, Aug. 1, 1936, *Victorin, Germain & Dominique 48996* (UO, UC, CIUC, G). RIMOUSKI CO.—Massacre Island, on conglomerate covered with moss, coniferous woods, Bic, Aug. 12, 1927, *Rousseau 26871* (US); same locality, June 30, 1927, *Rousseau 26401* (M, WS, G); humus in crevices of calcareous rock, July 8, 1905, *Collins & Fernald 85* (G, UC, NY, US). TEMISCAMING DIST.—Point-au-vent (Lake Temiscaming), June 25, 1918, *Victorin 8358* (M, G, US). WRIGHT CO.—Aylmer, May 26, 1901, *Fowler* (US).

ONTARIO: ALGOMA DIST.—waste ground by Algoma Central Railway, Gray (Mile 229), June 23, 1921, *Pease 18029* (G); ballast near Coppermine Point, Lake Superior, July 7, 1935, *Pease & Ogden 25161* (G). BRUCE CO.—Lion's Head, on damp calcareous rocks, June 11, 1932, *Victorin & Prat 45945* (RM, G). CARLETON CO.—vicinity of Ottawa, May 28, 1921, *Rolland 15761* (WS, NY, US). FRONTENAC CO.—Gardiner's Farm, near Kingston, June 10, 1897, *Langford* (M). LAMBTON CO.—on sides of sand hills, near Port Franks, May 24, 1906, *Dodge 1* (US). MANITOULIN CO.—dry cliffs, Gore Bay, Manitoulin Island, July 5, 1935, *Pease & Ogden 25190* (G, US). THUNDER BAY DIST.—rich shore of Lake Superior, about Lat. 48° 45′ N., Long. 87° 15′ W., 1 mi. n.e. of Schreiber, Aug. 16, 1937, *Hosie, Losee & Bannan 1413* (G); damp diabase ledge, Norma Creek, Thunder Cape, June 26, 1936, *Taylor, Losee & Bannan 504* (CIUC).

MANITOBA: MARQUETTE DIST.—Fort Ellice, along the line of the Grand Trunk Pacific Railway, June 27, 1906, *Macoun & Herriot* (G). PORTAGE LA PRAIRIE DIST.—Portage la Prairie, along the line of the Grand Trunk Pacific Railway, May 28, 1906, *Herriot* (G); Carberry, 1898, *Thompson* (M). DIST. UNCERTAIN—Piguitonay, Mile 214, route of Hudson Bay Railway, July 8, 1917, *Emerton* (G); Charleswood, June 5, 1915, *Thompson 97* (M).

SASKATCHEWAN: MOOSE JAW DIST.—newly burnt woods, Cypress Hills, June 15, 1884, *Macoun* (G). QU'APPELLE DIST.—moist woods, Qu'Appelle Valley, June 26, 1938, *Shevkenek 115* (G). DIST. UNCERTAIN—in rich, moist ground, usually in burnt-over ground, McKague, June 21, 1940, *Breitung 577* (M, IH, UT, NY).

ALBERTA: CALGARY DIST.—gravel banks and rocky hills, Shaganappi, vicinity of Calgary, 3400–3600 ft. alt., May 30, 1913, *Moodie 137* (NY, US). EDMONTON DIST.—burned area in woods, Edmonton, May 21, 1931, *Moss 2140* (WS). JASPER NAT. PARK—Jasper, 3472 ft. alt., Aug. 31–Sept. 2, 1943, *Scamman 3369* (G, US). MEDICINE HAT DIST.—moist, rocky woods, vicinity of Rosedale, 2200–2500 ft. alt., May 27, 1915, *Moodie 911* (M, CIUC, D, UT, NY, G, US). RED DEER DIST.—n. e. of Buffalo Lake, May 23, 1926, *Brinkman 2015* (US); Sarcee Reserve, June 15 to Aug. 15, 1905, *Goddard 489* (UC). ROCKY MTS. NAT. PARK—Bow River Valley, 4500 ft. alt., Banff, June 9–18, 1906, *Brown 62* (M, NY, G, US); roadside near the village, vicinity of Banff, 4500 ft. alt., June 19, 1899, *McCalla 2124* (NY, US). VICTORIA DIST.—grain field, Fort Saskatchewan, June 10, 1930, *Turner* (G). DIST. UNCERTAIN (probably ATHABASKA)—Athabaska Landing, July 28, 1914, *Hitchcock 12064* (US); Fort Chipewyan, Athabaska, June 5, 1903, *Preble & Cary 5* (US); muddy river bank along lower Firebag River near its mouth, June 3, 1935, *Raup 6033* (G); base of eastern slope of Caribou Mts., about 58° 57′ N., 113° 55′ W., and 58° 51′ N., 113° 57′ W., Wood Buffalo Park, Mackenzie Basin, July 17, 1930, *Raup 2439-a* (NY, US).

BRITISH COLUMBIA: CARIBOO DIST.—Alexis Creek, June, 1914, *Newcombe 19* (G). CASSIAR DIST.—above Discovery on road to Surprise Lake, July 10, 1930, *Setchell & Parks* (UC); near head of Ingenika River, Sept. 8, 1910, *Preble & Mixter 689b* (US); near head Iskut River, July 29, 1910, *Preble & Mixter 601* (US). KOOTENAY DIST.—near Goat Creek, 27 mi. n. of Natal, July 4, 1941, *Weber 2296* (M, RM, WS, NY, G); Kicking Horse Valley, vicinity of Field, 4000 ft. alt., June 20, 1906, *Brown 214* (M, NY, G, US). YALE DIST.—near Guichon Creek, 13 mi. s. of Savona, 50° 32′ N., 120° 52′ W., about 3500 ft. alt., June 23, 1941, *Hitchcock & Martin 7412* (M, RM, WS, UC, IH, NY, G); along Bolean Creek, about 1 mi. n.w. of Falkland, 2400 ft. alt., June 30, 1941, *Hitchcock & Martin 7485* (M, RM, WS, UC, IH, NY, G).

MACKENZIE: Fort Resolution, no date, *Onion, Kennicott & Hardisty* (NY).

YUKON: Fifty-Mile River, Aug. 4, 1899, *Bolton* (US); Dawson, June 3, 1914, *Eastwood 133* (WS, CIUC, G, US); recent burns, Fort Selkirk, June 13, 1899, *Gorman 1023* (NY, US); Klondyke, 1900, *MacLean* (US); Bonanza Creek, Aug. 11, 1899, *Tarleton 49b* (NY, US); Walker Gulch, July 16, 1899, *Williams* (NY); Lake Lebarge, June 23, 1899, *Tarleton 49a* (NY, US).

ALASKA: Eagle to Valdes trail, June 30, 1902, *Collier 73* (US); vicinity of Copper Center, 1908, *Heideman 66* (US); Hot Springs on the Tanana River, July 28, 29, 1909, *Hitchcock* (US); Yukon River country, no date, *Ketchum* (G); banks of railroad cut, Mt. McKinley Nat. Park, Aug. 2, 1939, *Nelson & Nelson 4010* (M, RM, NY, G); Fairbanks, June, 1927, *Palmer 1750* (US); Gopher Center, Copper River region, June 1, 1902, *Poto 14* (US).

### 9a. C. AUREA Willd. ssp. **occidentalis** (Engelm.) G. B. Ownbey, stat. nov.

*Corydalis aurea* var., Gray in Smiths. Contr. Knowl. 5:10. 1853 (Pl. Wright. 2:10).
*Corydalis montana* Engelm. apud Gray, Man. Bot. ed. 5. 62. 1867.
*Corydalis aurea* var. *occidentalis* Engelm. apud Gray, l. c. 1867; Bot. Gaz. 11:188. 1886.
*Capnoides montanum* Britton, in Mem. Torr. Bot. Club 5:166. 1894.
*Neckeria aurea occidentalis* Rydb. in Univ. Nebr. Bot. Surv. Nebr. 3:24. 1894.
*Corydalis crassipedicellata* Fedde, Rep. Spec. Nov. 10:364. 1912.
*Corydalis bilimbata* Fedde, l. c. 379. 1912.
*Corydalis chihuahuana* Fedde, l. c. 418. 1912.
*Corydalis curvisiliquaeformis* Fedde, l. c. 11:289. 1912.
*Corydalis Jonesii* var. *stenophylla* Fedde, l. c. 497. 1913.
*Corydalis pseudomicrantha* var. *Griffithsii* Fedde, l. c. 12:37. 1913.
*Corydalis pachyloba* Fedde, l. c. 38. 1913.
*Capnoides pachylobum* Greene ex Fedde, l. c. 1913, nom. nud. in synon.

Glaucous winter annual or biennial; stems often erect while young, usually 10–25 cm. or more long; basal leaves long-petioled; cauline leaves few, often some-

what reduced in size; leaf blades pinnate, having 5–7 pinnae, these pinnatifid and again incised; ultimate leaf segments usually oblong, 2–5 times longer than broad, subapiculate; peduncles usually stout; racemes surpassing the leaves at least in the early stages of growth, 5- to 20-, usually 8- to 12-flowered; bracts elliptical to linear, 10 mm. or less long, much reduced upward; pedicels erect, 1–5 mm. long; sepals scarious, fugacious, ovate, often toothed at the margin, 2 mm. or less long; flowers mostly bright yellow; spurred petal 14–18 mm. long, the hood usually not crested, the wing margin well developed, the blunt spur 5–9 mm. long, often somewhat globose at the tip; spurless outer petal 8–13 mm. long, geniculate, the hood and margin as in the spurred petal; inner petals 8–11 mm. long, the claw about one-half of the total length; stamen spur 3–6 mm. long; stigma about twice as broad as high; fruits 12–30, commonly 16–18 mm. long, erect, stout, curved upward and inward or obliquely along the floral axis, not moniliform; seeds about 2 mm. in diameter, black, acute at the edge, usually having a narrow marginal ring which is distinctly reticulate under magnification.

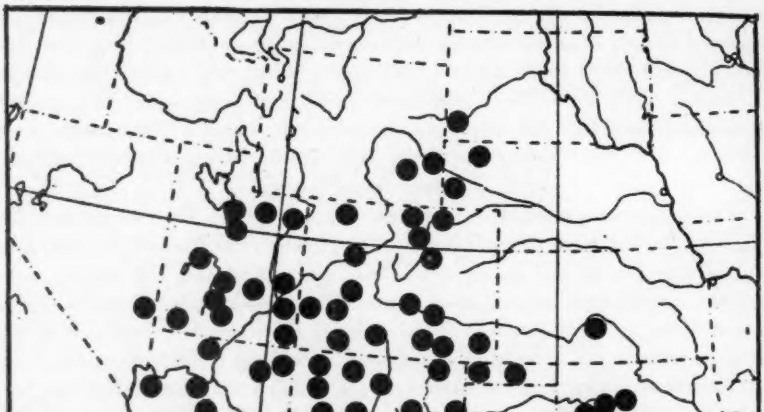
This subspecies is most often confused with ssp. *aurea.* The two are best distinguished by the more strongly monopodial growth form, stouter racemes, generally larger flowers and longer spurs, and, most important, the stouter, more strongly curved, erect or semi-erect fruits of ssp. *occidentalis.* In southwestern United States ssp. *occidentalis* is found at lower elevations as a general rule, but since the seeds of ssp. *aurea* often are washed down from the mountains the latter also sometimes is found at low elevations. The difference between the two represents a summation of several divergent tendencies which together form a rather reliable index to the proper disposition of any given specimen. At the same time the two are segments of a fundamentally heterogeneous species and true intermediates do exist.

Gray referred to this entity in the fifth edition of his 'Manual' but made no clear choice between the two names suggested by Engelmann, *C. aurea* var. *occidentalis* and *C. montana,* as he was undecided whether the plant represented a new species or variety. In 1866 Engelmann, in a letter to Gray (still preserved at the Gray Herb.), made the following statement: "If you retain *montana* as a species you must keep the name, I suppose, but as a variety of *aurea* the name of *occidentalis* is preferable . . .". In 1886, concluding that the entity was truly a variety of *C. aurea,* Gray accepted the name *occidentalis* and published *C. montana* as a synonym. In accordance with this point of view, there seems to be no doubt that the name *occidentalis* should be retained in its modified rank of subspecies.

The specimens cited by Gray in 1886 are of historical interest. Fendler's 1847 collections from Santa Fe, New Mexico, are cited first. These specimens appear to me to be typical but depauperate *C. aurea* ssp. *aurea.* The fact that they were first cited has led to their general acceptance as the historical type of *C. aurea* var. *occidentalis.* The second collection cited is *Wright 1309* from El Paso, Texas, which Gray said is better representative of the entity. This is quite true, and this collection is typical of the subspecies as understood today. Next cited is *Pringle*

*198* (later taken as the type of *C. chihuahuana* Fedde) which is again typical ssp. *occidentalis* as are Palmer's 1865 collections from Arizona (at least as to *Coues & Palmer 294*), and *Rusby 9* from the Burrow Mountains. The portion of *Hall & Harbour 31,* cited last, deposited in the Gray Herbarium, is true ssp. *occidentalis;* material bearing identical labels deposited in the Missouri Botanical Garden Herbarium and in the United States National Herbarium is ssp. *aurea.*

Loose, often sandy, dry soil, bottom-lands, prairies, plains, foothills and mesas, and



Map 12. Distribution of *Corydalis aurea* Willd. ssp. *occidentalis* (Engelm.) Ownbey.

along ditches, railroad embankments and washes, at elevations of about 1000–6500 feet; southwestern South Dakota and eastern Wyoming to western Oklahoma, Texas, northern Mexico, and Nevada. Flowers in spring at lower elevations, in summer at higher elevations, from about March 15 to July 30; fruits from about April 1 to August 15.

SOUTH DAKOTA: Fall River County.

NEBRASKA: Banner and Dawes counties.

KANSAS: Stafford County.

OKLAHOMA: Beckham, Blaine, Caddo, Canadian, Cimarron, Custer, Grady, Greer, Jackson, Jefferson, Kingfisher, Kiowa, Texas, and Tillman counties.

TEXAS: Childress, Comanche, Crosby, Culberson, Dickens, Fisher, Hall, Hudspeth, Jeff Davis, Kent, Lubbock, Nolan, Reeves, Scurry, and Sutton counties.

WYOMING: Albany and Platte counties.

COLORADO: Arapahoe, Archuleta, Baca, Boulder, Denver, Fremont, Garfield, Gunnison, Huerfano, La Plata, Larimer, Las Animas, Moffat, Montrose, Ouray, Pueblo, Rio Grande, and Weld counties.

UTAH: Duchesne, Emery, Garfield, Grand, Millard, Piute, Salt Lake, San Juan, Sevier, Uintah, Utah, and Washington counties.

NEVADA: Lincoln County.

ARIZONA: Apache, Cochise, Coconino, Gila, Graham, Maricopa, Mohave, Navajo, Pima, Pinal, Santa Cruz, and Yavapai counties.

NEW MEXICO: Catron, Colfax, Dona Ana, Eddy, Grant, Hidalgo, Luna, McKinley, Quay, Rio Arriba, Sandoval, San Juan, San Miguel, Socorro, Taos, Torrance, and Valencia counties.

CHIHUAHUA: Sept., 1934, *Dobie 13* (UT); Casas Grandes, June 2, 1899, *Goldman 433* (G, US); St. Diego, 6000 ft. alt., April 18, 1891, *Hartman 600* (NY, G, US); Chihuahua, spring, 1936, *LeSueur Mex-516* (UT); Majalca, June 24, 1936, *LeSueur 1207* (M, G); vicinity of Chihuahua, about 4250 ft. alt., April 8–27, 1908, *Palmer 4* (M, NY, G, US); valley near Chihuahua, March 22, 1885, *Pringle 198* (UC, NY, G, US—Isotypes of *C. chihuahuana* Fedde); 14 mi. s. e. of Minaca, 6500 ft. alt., July 25, 1937, *Shreve 8012* (UA); near Colonia Garcia in the Sierra Madres, 7300 ft. alt., July 25, 1889, *Townsend & Barber 163* (M, UC, NMA, NY, G, US—Isotypes of *C. crassipedicellata* Fedde); Santa Eulalia plains, 1885, *Wilkinson* (D).

DURANGO: San Ramon, April 21 to May 18, 1906, *Palmer 72* (M, UC, NY, G, US); Otinapa, July 25 to Aug. 5, 1906, *Palmer 399* (M, NY, G, US).

SINALOA: By spring water in shady canyon, near Platano, Sierra Monterey, March 9, 1940, *Gentry 5869* (M, UA, NY, G).

SONORA: Babispe, 5330 ft. alt., Dec. 24, 1890, *Hartman 358* (G); no definite locality, 1890, *Lloyd 369* (G).

STATE UNCERTAIN: Mexico, no date, *Coulter 664* (M, NY, G).

10. C. PSEUDOMICRANTHA Fedde, Rep. Spec. Nov. **11**:499. 1913

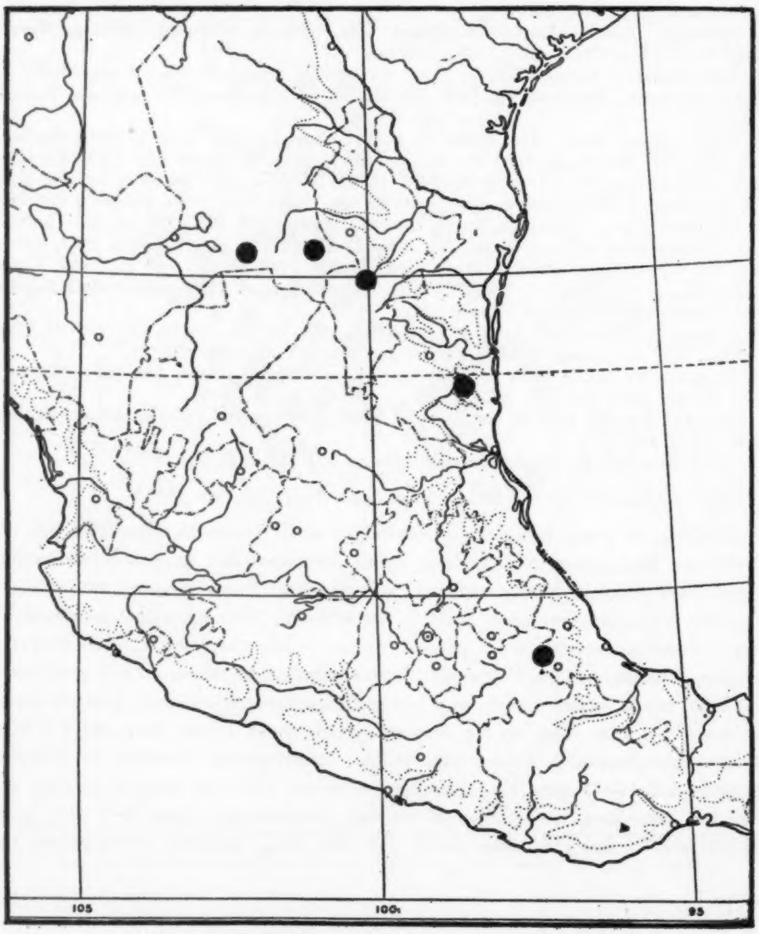
Glaucous or green biennial (or annual?); stems 1–several, sympodial, usually 20–40 cm. long, prostrate-ascending; basal leaves crowded, long-petioled; cauline leaves short-petioled, hardly reduced upward; leaf blades pinnate, the primary segments pinnatifid and again incised, the ultimate lobes elliptical, subapiculate; normal-flowered racemes, when present, 6- to 12-flowered; cleistogamous-flowered racemes abundant, 1- to 5-flowered; bracts elliptical to obovate, 2–8 mm. long, 1–5 mm. broad, often minute on cleistogamous-flowered racemes; pedicels erect, the lower 1–3 mm. long, shorter upward; sepals about 1 mm. long and 0.5 mm. broad, ovate-attenuate; flowers pale yellow, inconspicuous, crowded at anthesis; spurred petal 10–12 mm. long, the hood crestless, the wing margin narrow, the spur 3–4 mm. long, not globose at the tip; spurless outer petal 8–9 mm. long, slender, usually straight; inner petals 7–8 mm. long, narrowly oblanceolate, the

claw about two-fifths the total length; stigma 2-lobed, rectangular, twice as broad as high; fruits erect, commonly 25–30 mm. long, slender, straight or moderately curved; seeds about 2 mm. in diameter, black, submuricately decorated under magnification especially at the often distinct ring margin.

This subspecies is best distinguished by its slender, erect and usually straight fruits, in contrast to those of *C. aurea* ssp. *aurea* which are mostly pendent and curved. The presence of cleistogamous flowers suggests an affinity with *C. micrantha* but size and decoration of the seeds indicate that it is more properly maintained as a distinct species.

Mountains of southern Coahuila to Vera Cruz, Mexico, at elevations of about 7000–9500 feet. Flowers and fruits throughout the spring and summer months.

COAHUILA: Saltillo, Sept., 1898, *Palmer 356* (G, US); Sierra de Parras, 8000–9000 ft. alt., July, 1910, *Purpus 4602* (M, UC, G, US, TYPE).




Map 13. Distribution of *Corydalis pseudomicrantha* Fedde.

NUEVO LEON: Sierra Madre Oriental; lower San Francisco Canyon, about 15 mi. s. w. of Galena, 7500–8000 ft. alt., June 12, 1934, *Mueller &Mueller 773* (UT, G).
TAMAULIPAS: Canyon de Garrapata, April, 1926, *Runyon 1021* (G, US).
VERA CRUZ: Boco del Monte, Aug., 1908, *Purpus 3073* (M, UC, NY, G, US).

### INTRODUCED SPECIES

*C. lutea* DC, a European species, was collected at Elk Rock, Multnomah County, Oregon, *M. W. Gormon 4076,* June 2, 1917 (WS, D); *J. C. Nelson & M. W. Gormon 1259,* same date (G). Gormon made the following comment on the label: "Com. Probably esc. from cultivation. Native of S. Eur. where it runs wild as a weed." This apparently is the only recorded instance of a native European or Asiatic species having escaped from cultivation in the United States. Doubtless it has happened other times, as many Eurasian species are attractive horticultural curiosities and have been grown in this country. Sporadic occurrence of such species or of weedy species accidentally introduced is to be expected.

*C. lutea* has the following characteristics: Leaves thrice ternately compound or incised, the ultimate segments elliptical; flowers yellow, the spur about one-fourth the total length of the spurred petal; fruit about 10 mm. in length, long-pedicellate.

### EXCLUDED SPECIES

*Corydalis biaurita* Hornem. Hort. Hafn. **2**:668. 1815 = DICENTRA sp.

*C. bracteosa* Spreng, Syst. Veg. ed. 16. **3**:162. 1826 = DICENTRA sp.

*C. canadensis* Goldie, in Edinb. Phil. Jour. **6**:329. 1822 = DICENTRA CANADENSIS (Goldie) Walp.

*C. Cucullaria* Pers. Syn. Pl. **2**:269. 1807 = DICENTRA CUCULLARIA (L.) Bernh.

*C. eximia* Link, Enum. Hort. Berol. **2**:218. 1822 = DICENTRA EXIMIA (Ker) Torr.

*C. formosa* Pursh, Fl. Am. Sept. **2**:462. 1816 = DICENTRA FORMOSA (Andr.) DC.

*C. fungosa* Vent. Choix de Pl. *t. 19.* 1803 = ADLUMIA FUNGOSA (Ait.) Greene.

*C. ochotensis* Turcz. Reported from Sitka, Alaska, by Regel, in Bull. Soc. Mosc. $34^3$:142. 1861. This species actually does not occur in America.

*C. paeoniaefolia* Pers. Syn. Pl. **2**:269. 1807. Listed as a questionable synonym of *C. Scouleri* Hook., Torrey and Gray, Fl. N. Am. **1**:69. 1838. This Asiatic species actually is not found in America.

*C. tenuifolia* Pursh, Fl. Am. Sept. **2**:462. 1816 = DICENTRA sp.

---

### INDEX TO EXSICCATAE

The collector's numbers are printed in *italics*, or if the collection is unnumbered, it is indicated by a dash following the collector's name. The numbers in parentheses are those assigned to the species and subspecies in this revision.

Allen, O. D. *118, 311a* (1).
Ames, Mrs. M. E. P. — (2).
Anderson, D., Rhinehart, & Nelson. *849* (9a).
Anderson, E., & D. M. Anderson. *26039* (4).
Anderson, F. W. *274* (9).
Anderson, J. P., & G. W. Gasser. *7320* (4).
Anderson, J. R. — (1); — (4); *804* (9).
Anderson, W. A. *400* (5).
Anect, Bro. *51, 167* (9).
Applegate, E. I. *8517, 8610* (9); *8450* (9a).
Armstrong, M. *515* (1).
Arsène, Bro. G., & Bro. A. Benedict. *15144* (9).
Arthur, J. C. — (7).
Artz, L. *523* (4).
Ashe, W. W. — (4).
Austin, Mrs. R. M. —, *557, 1393* (2); — (9).
Averill, H. — (4).

Bacigalupi, R. *1628* (2); *2146* (4); *978* (9).
Bailey, L. H. Jr. — (9).
Bailey, W. W. — (4).
Baker, C. F. *258, 339, 716* (2a); — (4); *349, 517* (9); *183, 338, 340* (9a).
Baker, C. F., F. S. Earle, & S. M. Tracy. *304, 910* (9).
Baker, M. S. *4532G, 9374* (9).
Bannister, H. M. — (3).
Barber, H. S. *115* (9a).
Barber, M. A. *167, 257* (9).
Barkley, E. D. *96* (7a).
Barkley, F. A. — (7a).
Barkley, Mrs. M. W. — (7).
Barlow, B. — (4).
Barndell, E. M. — (1).
Barnhart, J. H. *31, 443, 793, 1018* (4); *474* (9).
Bartlett, Mrs. F. *55* (9).
Bartlett, H. H. —, *251* (4).
Bartlett, Mrs. W. H. *292* (9).
Bartram, E. B. — (9).
Bates, J. M. — (9a).
Beal, W. J. — (4).
Bebb, M. S. — (9).
Bebb, R. *2736, 3763, 3916, 5093* (6); *1446* (7a); *2362* (8).
Bell, J. M. — (4).
Bell, W. B. *1460* (9).
Benke, H. C. *5492* (6); *5141* (7); *3338, 5824* (7a)
Benner, W. M. — (4); *5013* (9).
Bennett, F. L. *364* (9).
Benson, L. *1429* (1); *2202* (2).
Benson, S. B. *72* (9).
Bereman, S. D. *704* (9).
Bergman, H. F. — (9).
Berlandier, J. L. *1799* (7a); *548, 1799, 1933* (7b); *216, 1476* (8).
Berry, R. E. *82* (9a).
Bertaud, Bro. 55 (9).
Bethel, E. — (2a).
Bethel, E., F. S. Willey, & I. W. Clokey. *4128* (2a).
Bidwell, Mrs. J. — (2).
Billings, W. D. *903* (5).
Biltmore Herb., *1291* (4); *2082a* (5); *5453a* (7a); *2079a* (9).
Bissell, C. H. — (4).
Blaisdell, F. E. *67* (3).
Blake, S. F. *9320* (5).
Blanchard, F. — (4).
Blankinship, J. W. —, *661* (9).
Blankinship, Laura A. — (8a).
Blomquist, H. L. *3714* (4); *3713, 7295* (5); *10228* (7a).
Blomquist, H. L., & D. Correll. *4710* (4).
Bogusch, E. R. —, *598, 601* (7a); *600* (8).
Bolton, A. L. — (9).
Booker, J. — (9a).
Bostock, H. *60* (4).
Bourgeau, E. — (4).
Bowman, P. W. *247* (4).
Boyd, A. A. — (4).
Brackett, E. — (7a).
Brady, A. W. — (4).
Brainerd, E. — (9).
Brandegee, T. S. —, *1097, 4263, 13233* (2a); *620* (9); *36, 284* (9a).
Brass, L. J. *14175* (9a).
Braun, E. L. — (5).
Bray, W. L. — (7a); *75* (8).
Breitung, A. J. —, *577* (9).
Briggs, F. P. *1458* (4).
Brigham, Mrs. R. H. *13730* (9).
Bright, J. *14931* (4); *14281, 14283* (5).
Brinkman, A. H. *4436* (4); *2015, 4114a, 5253* (9).
Britton, N. L. — (5).
Britton, N. L., E. G. Britton, & A. M. Vail. — (4).
Broadhead, G. C. — (6); — (7).
Brooks, H. E. — (4).
Brown, A. H. *37* (6).
Brown, S. *62, 214* (9).
Bruce, Mrs. C. C. —, *1192* (2); *2206* (9).
Bruhin, T. A. — (7).
Bryan, W. C. *74* (9).
Bryant, Mrs. — (3).

Deam, C. C. *31641* (4); —, *12574* (5).
Degener, O. *4841* (9a).
Degener, O., & L. Peiler. *16790* (9).
Demaree, D. *4732, 10594, 12059* (5); *3039, 12111, 15095, 20884, 20885, 20920, 22023* (6); *14516, 20870* (7a); *11898, 12351, 12547* (8a); *7470, 12193* (9a).
Dewey, L. H. *1* (4); *225* (5).
Dixon, J. *17, 25* (3); *45* (4).
Dobie, Mrs. B. McK. *13* (9a).
Dodge, C. K. *43* (5); *1* (9).
Dougan, L. M. — (7).
Downey, J. *1818* (9).
Doyel, Mrs. — (7).
Drouet, F. — (6); *364* (7).
Drummond, T. *16* (7a).
Drushel, J. A. *1387* (4); —, *4059, 4994* (5); *1819* (9).
Duran, V. *3069* (9).
Dutton, D. L. — (4); — (9).
Dwight, N. E. *9* (9a).

Ealy, R. *20* (6).
Eames, A. J., & L. H. MacDaniels. *2366, 2367* (9).
Earle, F. S. *503, 503a, 643* (9); — (9a).
Earle, F. S., & S. M. Tracy. *135, 392* (8).
Earle, R. E. — (4).
Eastwood, A. *1758* (2); — (2a); *307, 380* (3); *133* (9); *6093, 8204* (9a).
Eaton, D. C. — (7a).
Eaton, D. W. — (3).
Eby, A. F. — (4); — (5); — (9).
Eby, J. H. — (4); — (9a).
Edie, M. C. *2* (9).
Edmonds, H. W. — (4).
Edmondson, T. W. *1106, 4995* (4).
Edwards, O. T. — (1).
Eggert, H. — (5); — (7); — (7a); — (7b); *106* (8a).
Eggleston, W. W. *5656* (2a); *3015* (4); *10439, 11955, 18674, 20251* (9); *6402, 6427, 6447, 14322, 19825, 19982* (9a).
Eggleston, W. W., & M. L. Fernald. — (4).
Ehlers, J. H. *252, 6208* (4); —, *7558* (9).
Ellis, C. C. *6* (9).
Elmer, A. D. E. —, *1018* (9).
Elmore, F. H. *8* (9a).
Elrod, M. J. *51* (9).
Emerton, J. H. — (4); — (9).
Emig, W. H. *520* (7).
Engelmann, G. — (1); — (4); — (5); —, *132* (6); — (7); — (9).
Engelmann, H. — (9a).
Engleman, J. *1569, 1571* (7); *213, 1570, 1572* (8a); *1566, 1567, 1568, 1695* (9a).
Epling, C. *6371* (1); *5842* (7).
Epling, C., & J. M. Houck. *9358* (2d).
Epling, C., & W. Robison. — (2).
Eskew, C. T. *1557* (7); *1585* (8a); *203, 243* (9).
Evans, W. J. *43* (6).
Eyles, D. E. *7725* (5).

Fassett, N. C. *3853* (4); *20937* (5); *20113* (7).
Fassett, N. C., & W. C. Meyer. *5717* (7).
Faxon, C. E. — (7a).
Faxon, E., & C. E. Faxon. — (9).
Fendler, A. *17* (9).
Fendler, F. S. *1445* (4).
Fernald, M. L. — (4).
Fernald, M. L., & J. F. Collins. *1050* (9).
Fernald, M. L., & H. B. Jackson. *12098* (4).
Fernald, M. L., & J. B. Lewis. *14536* (5).
Fernald, M. L., & B. Long. *23865, 23866* (4); *7041, 11838, 12083* (5).
Fernald, M. L., B. Long, & E. C. Abbe. *14157* (5).
Fernald, M. L., B. Long, & A. S. Pease. *11685, 11686, 11687* (5).
Fernald, M. L., & A. S. Pease. *25088* (4).
Fernald, M. L., & H. St. John. *7502* (5).
Fernald, M. L., & W. C. Strong. *429* (4).
Fernald, M. L., & K. M. Wiegand. *5455, 5456* (4).
Fernald, M. L., K. M. Wiegand, & A. J. Eames. *14295* (4).
Ferris, R. S., & R. Duthie. *1002* (2c); *1068* (9).
Fiero, K. *23* (9).
Fiker, C. B. *1674* (9).
Fink, B. — (7).
Fisher, G. L. — (7a).
Fisher, H. L. — (4).
Fitzpatrick, T. J., & M. F. L. Fitzpatrick. *1* (7).
Flint, M. B. — (5).
Flodman, J. H. *486* (9).
Fogg, J. M. Jr. *4984, 13459, 14552, 15115,* (4); *1579* (5).
Fordwood, W. H. *139, 365* (9).
Foster, R. C., & J. F. Arnold. *199* (9a).
Fowler, J. — (4); — (9).
Freeborn, R. *338* (7b).
Freeman, O. M. — (4); — (7a).
French, G. H. — (5).
Friesner, R. C. *2726, 8528, 16649* (5).
Frye, W. M. — (4).
Fuller, T. O. — (7a).
Fulton, H. J. *7165* (9a).

Galway, D. *8415* (9a).
Garrett, A. O. *5498*, *8453* (9); *2555* (9a).
Garvin. — (9a).
Gary, L. B. *575* (5).
Gates, F. C. *12453* (4); *10205* (5).
Gates, F. C., & M. T. Gates. *10368* (4).
Gayle, E. E. — (7).
Gentry, H. S. *5869* (9a).
Geyer, A. — (5).
Gilbert, F. A. *43* (5).
Gilbert, F. A., L. O. Williams, & C. Smithson. *404* (5).
Gilbert, G. — (4).
Gilbert, J., & T. Gilbert. — (4).
Gilman, M. F. *47* (9a).
Girard. — (8).
Glatfelter, N. M. — (4); —, *61* (5).
Gleason, H. A. *9723* (4); — (5).
Glismann, D. *42* (9a).
Goddard, P. E. *489* (9).
Godfrey, R. K., & R. N. White. *7054* (7a).
Goldman, E. A. *433* (9a).
Goodale, A. S. *69962* (7a).
Goodding, C. O. *6429* (9).
Goodding, L. N. *69*, *69a*, *1027*, *1189*, *1223*, *1315*, *1501*, *2071* (9); *931* (9a).
Goodman, G. J. *2533* (6).
Goodman, G. J., & C. L. Hitchcock. *1205*, *1484* (9).
Goodman, G. J., & L. B. Payson. *2840* (9a).
Gorman, M. W. *1023* (9).
Gould, L. — (7a).
Grace, M. C. *152* (8a).
Graham, E. H. *3771*, *8635*, *9287* (9); *7882*, *8014* (9a).
Grant, A. L. *1645* (5).
Grant, G. B. *132*, *2726* (9).
Grant, J. M. —, *7936* (1).
Grant, M. L. *2845* (4); *2846* (9).
Grassl, C. O. *3766* (4).
Graves, E. W. —, *1757* (7).
Gray, A. — (9); — (9a).
Gray, F. W. *5134* (4).
Greenman, J. M. *235*, *236*, *238*, *372* (4); *3958*, *4212* (5); *2184*, *3392* (9).
Greenman, J. M., O. E. Lansing Jr., & R. A. Dixon. *132* (4).
Griffith, H. R. *35* (5).
Griffiths, D. — (9); *2280*, *2379*, *2648*, *3553*, *3846*, *4176* (9a).
Griscom, L. — (4).
Grout, A. J. — (4).

Haberer, J. V. *55* (4).
Hale, J. — (7a).
Hall, D. *8415*, *8506* (9a).
Hall, E. — (7); *11* (7a).
Hall, E., & J. P. Harbour. *31* (9, 9a).
Hall, H. M. *9308*, *9796* (2).
Hall, H. M., & E. B. Babcock. *4291* (2).
Hamilton, L. P. — (9a).
Hanna, G. D. — (3).
Hanson, H. C. —, *364* (8); *A108*, *C363* (9a).
Hanson, H. C., & E. E. Hanson. *A1179*, *A1180* (9a).
Hardin, E. — (9).
Harper, D. C. — (2a); — (9).
Harper, F. *53* (4).
Harper, R. A. — (4).
Harper, R. M. *3296* (5); *10* (6).
Harper, R. M., & H. Kurz. — (7a).
Harrington, G. L. *57* (3).
Harrington, H. D. *1621* (2a); *3* (9).
Harris, M. *3605* (9).
Harrison, B. F. *113*, *6158*, *7471*, *9163*, *10165* (9); *6399*, *9630*, *10155* (9a).
Harrison, G. J. *7894* (9).
Harrison, J. J. — (7b).
Hartman, C. V. *358*, *600* (9a).
Harvey, F. L. —, *1*, *4*, *16*, *125** (6); — (7).
Harvey, F. L., & L. H. Harvey. — (4).
Hasse, H. E. — (7a).
Hastings, G. T. — (4).
Havard, V. — (7a); — (8); — (9a).
Hayden, A. *5045*, *5047*, *5056*, *11246*, *11247* (7).
Hayden, F. V. — (5); — (7); *56* (9); — (9a).
Hawk, H. A. — (6).
Hayward, H. E. *638*, *645*, *1335* (9).
Heald & Wolf. *711* (8).
Heath, H. — (3).
Hedrick, D. C. *252* (8).
Heideman, C. W. H. *66* (9).
Heidenreich, V. T. *193* (9).
Heller, A. A. *12047*, *14685*, *16284* (2); —, *9* (4); —, (5); *1433* (7a).
Heller, A. A., & E. G. Halbach. *1209* (4).
Heller, A. A., & E. G. Heller. *3871* (1); *3500*, *3529* (9); *3515* (9a).
Henderson, J. B. *33*, *5689* (6).
Henderson, L. F. *49*, *546 of 1924* (1); *3265* (2c); *3716* (9).
Hermann, F. J. *7290*, *7529*, *7748*, *8729* (4); *10087* (7a); *5247*, *7749* (9).
Herrick, C. L. *259*, *524*, *1006* (9).
Herriot, W. — (9).
Hershey, A. L. *3971*, *3972*, *3974*, *3978*, *3980* (9); *3973*, *3975*, *3976*, *3977*, *3979* (9a).
Hexamer, F. M. — (4).

Lighthipe, M. L. — (4).
Lindheimer, F. L. —, *433*, *546*, *663* (8).
Lindsay, A. A. *4556* (1).
Little, C. S. *1* (9).
Little, E. L. Jr. *54*, *1023* (5); *123*, *651*, *1022*, *1024* (6); *534* (9a).
Little, Mrs. E. L. *1021* (5); *1020* (7a).
Little, E. L., & Mrs. E. L. Little. *119* (5).
Livingston, G. A. *47* (2a).
Livingston, R. B. *175*, *301* (9).
Lloyd, C. E. *369* (9a).
Lloyd, C. G. — (5).
Lloyd, F. E. — (1); — (4).
Lodewyks, M. C. *87* (7).
Loest, E. — (8a).
Long, B. *50047* (4); *42948*, *56265* (5).
Loomis, H. F. *926* (9a).
Lucas, W. D. *242*, *245* (9).
Lucas, W. D., J. T. Painter, & F. A. Barkley. *14236* (8).
Luckhardt, R. *185* (7).
Lunell, J. — (9).

McAtee, W. L. *3227* (4); *3451* (7a).
McBryde, J. B. — (7a); *M1007* (8a).
McCalla, W. C. *2124* (9).
McCart, W. L. *985* (6); *1569-2* (8a).
McCauley, Lt. — (2a).
McClellan, B. *10* (7).
McClellan, J. T. *12* (7).
McCree, J. *633* (5).
McCubbin. — (5).
McDonald, F. E. — (7).
McFarland, F. T. *22* (4).
McIntosh, A. C. *138* (9a).
McKelvey, S. D. *1686* (7a); *2000* (8); *2402*, *4802* (9); *4330*, *4438* (9a).
McLean, D. *27* (6).
McMullen, E. — (6).
McMurry, F. B. *655* (8a).
McVaugh, R. *4950* (4); *4906* (5).
Macbride, J. F. *595* (2c).
Macbride, J. F., & E. B. Payson. *3287*, *3457* (9).
MacDougal, D. T. *250* (9); *83*, *105*, *114* (9a).
Macfadden, F. A. *15514* (2c).
MacIntyre, Mrs. — (3).
Mackaness, F. — (4).
Mackenzie, K. K. *677*, *2612* (4); —, *5756* (5); —, *17*, *25*, *33*, *50* (7); *58* (9).
MacLean, J. — (4); — (9).
Macoun. —, *99* (4); *7*, *112* (5); —, *100* (9).
Macoun, J. M. — (3); — (4); — (9).
Macoun, John. — (4); — (5); — (9).
Macoun, John, & W. Herriot. — (9).
Maguire, B. *861a*, *3460* (9).
Maguire, B., & H. L. Blood. *1364*, *1863* (9a).
Maguire, B., & G. Piranian. *12478* (2a).
Maguire, B., & J. D. Redd. *1862* (9).
Manning, W. H. — (9).
Marcelline, Sister M. *2063* (9).
Marie, P. Louis. — (4).
Marshall, W. F. *475* (9a).
Martin, B. — (7a).
Mason, H. L. — (3); *3423*, *3473* (9).
Mason, R. F. *61*, *85*, *87* (6); — (7).
Massey, A. B. *849* (4); *1749*, *3799* (5).
Mathias, M. E. *143* (4); *386*, *593* (9).
Maxon, W. R. *75* (5).
Maxon, W. R., & T. R. Robinson. *3* (4).
Maxon, W. R., & P. C. Standley. *253* (5).
Mearns, E. A. — (7); *278*, *566*, *1045*, *1265*, *3790*, *4968* (9); —, *305* (9a).
Mearns, E. W. *57*, *58* (4).
Memminger, E. R. — (4).
Mendenhall, W. C. — (3); — (4).
Mericle, L. *449* (9a).
Merrill, E. D., & E. N. Wilcox. *646* (9).
Mertie, J. B. *60* (3).
Mertz, H. N. — (5).
Metcalfe, O. B., *877*, *980* (9); *19*, *1050* (9a).
Metz, Sister M. C. *2151* (8).
Mexia, Ynes. *2040* (3); *2106*, *2240* (4).
Meyer, F. G. *468*, *2159* (1).
Miller, A. — (2c).
Miller, G. S. Jr. *443* (7a).
Miller, W. N. *86* (4).
Milligan, Mrs. J. M. — (6).
Millspaugh, C. F. *446* (4); *14* (5).
Minshall, W. H. *42* (9).
Moffatt, W. S. *353*, *413* (4).
Mohr, C. — (5); — (7a).
Moldenke, H. N. *8768* (4); *2455* (5); *1981*, *8204* (9).
Moodie, M. E. *137*, *911* (9).
Moore, A. H. *1667* (4); *5092* (5).
Moore, E. J. — (9).
Moore, F. L., & C. E. Moore. — (4); — (7); — (9).
Moore, H. E. Jr. *625* (7a).
Moore, J. A., & J. A. Steyermark. *3065*, *3664* (9).
Moore, J. W., & B. O. Phinney. *12372* (7).
Moore, J. W., & C. O. Rosendahl. *13351* (9).
Moritmer, M. F. *83* (5).
Morton, M. D. *200* (6).
Moseley, E. L. — (5).

Peebles, R. H., & E. G. Smith. *11555* (9).
Penard, E. *39* (9).
Penfound, W. T. — (5); — (7); — (7a).
Pennell, F. W. *5761* (9a).
Perrin, L. —, *77* (6).
Perry, R. C. — (6).
Phelps, O. P. *490* (4).
Pickett, R. *64* (9).
Piper, C. V. —, *19, 4958* (1); *4057* (2d); —, *2253* (9).
Piper, R. H. *112, 1525* (4).
Plank, E. N. — (6); — (7a).
Pollard, C. L. *48, 136* (5).
Pollock, W. M. — (4).
Polson, M. *19* (6).
Poole, S. F. *121* (7).
Porsild, A. E., & R. T. Porsild. *135, 739* (4).
Porter, C. L. *3045* (9); *2858* (9a).
Poto, W. L. *121* (4); *14* (9).
Preble, A. E., & M. Cary. *13* (4); *5* (9).
Preble, E. A., & G. Mixter. *619* (3); *601, 689b* (9).
Preble, E. A., & A. E. Preble. *91* (4).
Pringle, C. G. —, *198* (9a).
Pulling, H. E. — (4).
Purpus, C. A. *6550* (9); *7058* (9a); *3073, 4602* (10).
Pusonett, K. *59* (7a).

Quarterman, E. *709, 1094* (5).
Quick, C. R. *1072* (2d).

Radford & Stewart. *32* (7a).
Ramaley, F. *1165, 1413* (9).
Ramaley, F., & K. R. Johnson. *14731* (9).
Ramaley, F., & Richards. *15960* (9a).
Ramaley, F., & W. W. Robbins. *2465* (9).
Rand, E. L., & B. L. Robinson. *121* (4).
Randel, W. *21* (7).
Randolph, L. F., & F. R. Randolph. *1143* (4).
Raup, H. M. *2443-a, 6088, 6115, 7624* (4); *2438-a, 2439-a, 2440-a, 2442-a, 6033, 6052* (9).
Raup, H. M., & E. C. Abbe. *4473, 4531, 4595* (4).
Redfield, J. H. —, *287, 288* (4); *279, 280, 281* (5); *283* (9).
Reed, E. L. *1825* (8).
Reed, J. F. — (4).
Reed, J. F., & M. S. Reed. — (7a).
Reppert, F. — (8a).
Reverchon, J. —, *2736, 3711, 4357* (6); *1896* (7); —, *1896, 2735, 2963, 3710* (7a); —, *3707, 3709* (8); — (8a).
Reynolds, H. C. *1419, 2968, 2981, 3059, 3327, 3846* (7).
Rhoades, W. — (4).
Rice, E. *37* (8a).
Ricker, P. L. — (4).
Rickett, H. W. *496* (5); *466* (7).
Riedel, M. — (7a).
Riehl, N. — (7).
Rinehart, F. *210* (7a); *234* (8a).
Robbins, W. W. *4896* (9).
Robinson, B. L. —, *80* (4); *251* (7a).
Robinson, T. R., & W. R. Maxon. *3* (4).
Rodgers, L. *343* (4).
Roland, A. E. *41416* (4).
Rolland, Fr. *7150, 15761* (9).
Rollins, R. C. *2003* (2a); *1963* (9).
Rose, J. N., & J. H. Painter. *8128* (4).
Rose, J. N., W. R. Fitch, & T. H. Parkhurst. *17710* (9).
Rose-Innes, R. *41022* (7a).
Rosendahl, C. O., & F. K. Butters. *1565* (1); *3193* (7).
Rossback, G. B., & R. P. Rossback. *476* (1).
Rothrock, J. T. *22, 28* (9).
Rousseau, J. *25264, 26971* (4); *26401, 26592, 26657, 26871* (9).
Rowlee, W. W., K. M. Wiegand, & G. T. Hastings. — (4).
Runyon, E. *47* (8a, 9a).
Runyon, R. *1618* (7b); *1021* (10).
Rupp. — (5).
Rusby, H. H. *282, 291* (4); *9* (9a).
Russell, C. — (7); — (7a).
Rust, H. J. *621* (9).
Ruth, A. *361* (4); *194, 228, 231, 233, 363, 1674, 1841* (5); *1175* (6); *1053* (7a); *3* (9a).
Rutter, C. —, *92, 179, 206* (3).
Rydberg, P. A. *6848* (2b); *8191, 9239, 9653* (4); *125, 512, 513* (9); *10, 513* (9a).
Rydberg, P. A., & A. O. Garrett. *8873* (9); *9208* (9a).
Rydberg, P. A., & R. Imler. *403* (6).
Rydberg, P. A., & R. K. Vreeland. *6262, 6263* (9); *6261* (9a).

Safford, H. T. — (5).
Safford, P. — (2).
Safford, W. E. *116* (4).
St. John, H. *8662* (1); *6361, 7629* (9).
St. John, H., & B. Long. *1030* (5).
St. John, H., & D. White. *22* (4).
St. John, Mrs. O. — (9a).
Sandberg, J. H. —, *163* (4); —, *18, 434, 1025* (9).

Taylor, B. 2301 (9).
Taylor, B. C. — (4).
Taylor, T. M. C., R. C. Hosie, R. E. Fitzpatrick, S. T. Losee, & A. Leslie. 1310, 1311 (4); 1314 (9).
Taylor, T. M. C., S. T. Losee, & M. W. Bannan. 505, 506, 508 (4); 502, 504 (9).
Taylor, K. A. — (5).
Texas, University of. — (7a); — (8); — (8a); — (9); — (9a).
Thames, L. — (9a).
Tharp, B. C. — (6); —, 35000, 37000 (7a); — (7b); —, 36000, 37001 (8).
Thompson, E. — (1).
Thompson, E. S. — (9).
Thompson, J. W. 630, 4110, 9409 (1); 13406 (2c); 7000, 8311, 11447, 11905, 13502, 14162 (9).
Thompson, J. W., & E. M. Thompson. 42, 209 (9).
Thompson, S. L. 30 (4); 97 (9).
Thornber, J. J. — (7); —, 5699 (9); —, 2822, 4053 (9a).
Thornber, J. J., & Brown. — (9a).
Thornber, J. J., & F. Shreve. 7809 (9).
Thornton, C. W. 319 (3).
Thousen, Mrs. O. T. 6 (3).
Thurber, G. 146 (9a).
Tidestrom, I. 3500, 3776 (2a); 333, 1879, 9468, 10935 (9).
Timmerman, M. — (4).
Tinsley, J. D. — (5).
Tolstead, W. L. 6898, 7074 (8).
Topping, D. L. — (4).
Tosh, J. P. 564 (4); 97 (5).
Toulouse, B. — (9a).
Toumey, J. W. 49 (9a).
Townsend, C. H. T., & C. M. Barber. 163 (9a).
Townsend, E. C. — (1).
Tracy, S. M. 9212 (7a); 37 (9a).
Tracy, S. M., & F. S. Earle. 392 (8).
Train, P. 2176, 2616, 3053 (9); 2536 (9a).
Trelease, W. — (4); —, 107 (5); — (9).
Trelease, W., & D. A. Saunders. 3872, 3873, 3874 (3).
True, F. W., & D. W. Prentiss Jr. 12 (3).
Tufte, E. T. 101 (9).
Turner. 167 (9).
Turner, G. H. 4 (9).
Tweedy, F. 429 (5); 136 (8); 123, 3534, 4949, 4951 (9); 4950, 5536 (9a).
Tyler, A. A. — (4).
Tyler, E. E. — (7).

Umbach, L. M. —, 706 (4); — (5).
Underwood, L. M., & A. D. Selby. 208 (9).

Van Eseltine, G. P. 251, 282 (5).
Van Valkenburgh, A. N. 9 (6).
Vasey, G. R. — (4).
Vestal, A. G. 262 (9a).
Victorin, Marie. 206, 8365, 10055, 11328, 15757, 15760 (4); 8358 (9).
Victorin, Marie. & H. Prat. 45945 (9).
Victorin, Marie, & Roland-Germain. 33122, 49743 (4).
Victorin, Marie, Rolland-Germain, & Dominique 260 (4); 48996 (9).
Victorin, Marie, Rolland-Germain, J. Rousseau, & R. Meilleur. 40082 (4).
Vinson, Dr. — (5).
Visher, S. S. 4021 (7); 152 (9).
Volk, E. — (5).
Vreeland, F. K. 916 (4).

Waghorne, A. 21 (4).
Wagner, R. — (3).
Wahl, H. A. 676 (4); 563 (5).
Waite, M. B. — (4).
Waldron, C. B. — (9).
Walker, — (5).
Walker, E. H. 2280, 2464 (4).
Walker, E. P. 254 (9); 146 (9a).
Walpole, F. A. 1457, 1467 (3).
Ward, C. G. 16 (7a).
Ward, L. F. 64, 520 (5); 3 (9a).
Warnock, B. H. 57, 46022 (7a); 63, 423, 472, 20621, 21397, 46021 (8); T135 (8, 9).
Warren, E. R. 1846 (2a); 1794 (9).
Washburn, E. W. — (7).
Waterfall, U. T. 621 (6); 2615 (7a); 410, 2591 (8a); 3277 (9); 2030 (9a).
Watson, S. 27 (2d); — (4); 26, 53 (9); 52 (9, 9a).
Watt, D. A. — (4).
Weatherby, C. A. 6088 (7a).
Weatherby, C. A., & L. Griscom. 16532 (7a).
Webb, R. J. — (4).
Weber, W. A. 2600 (4); 2296 (9).
Wehmeyer, L. E., F. N. Martin Jr., & H. F. Loveland. 5003a (9).
Wells, Mrs. E. M. 67 (6).
Werkenthin, F. C. — (9a).
Wetherill, A. — (9).
Wheeler, C. F. — (9).
Wheeler, H. N. 517, 2622 (9a).
Whetzel, H. H. — (5).
White, M. — (7).

## Index to Scientific Names

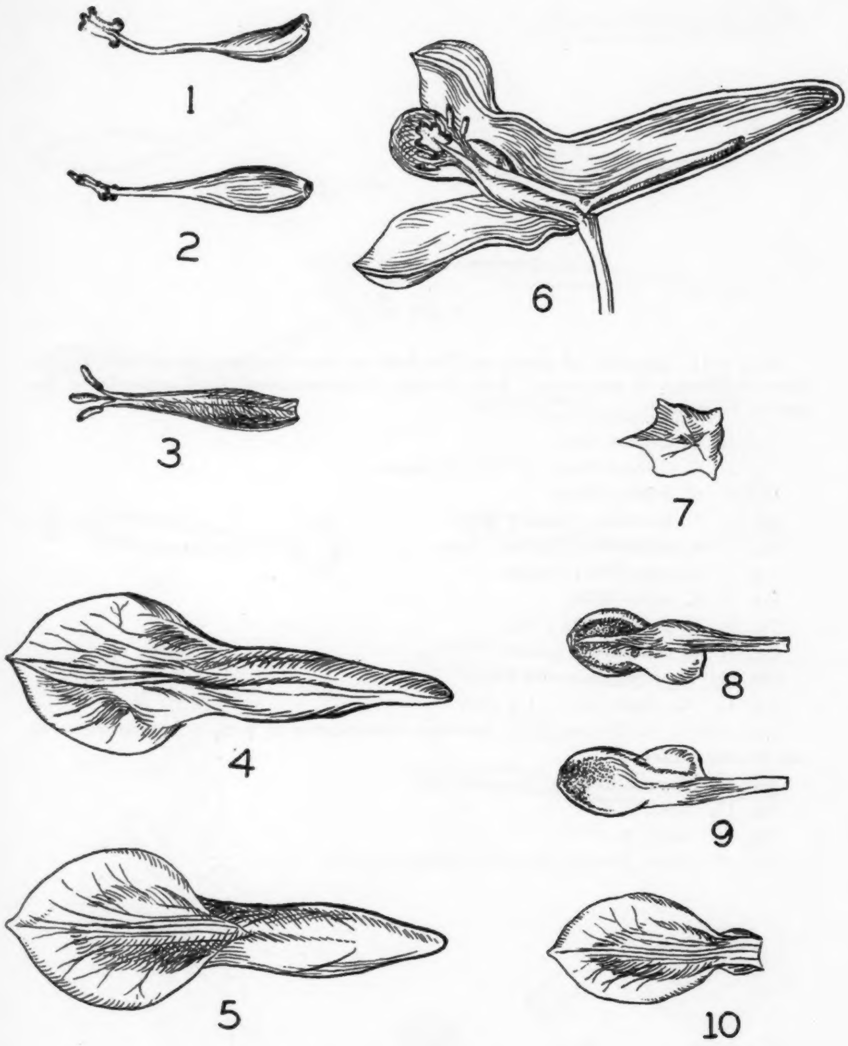
Previously published names accepted here are in Roman type; new names, combinations, and the page numbers on which the taxonomic treatment appears are in **bold face**; synonyms are in *italics*.

## Explanation of Plate

### PLATE 28

Generalized floral morphology of *Corydalis* drawn from *C. Caseana* Gray ssp. *Brandegei* (Wats.) Ownbey.

Fig. 1. Dorsal view of gynoecium.
Fig. 2. Lateral view of gynoecium.
Fig. 3. Unspurred stamen phalange.
Fig. 4. Exterior view of spurred petal.
Fig. 5. Interior view of spurred petal.
Fig. 6. Internal structure of flower showing arrangement of parts.
Fig. 7. Sepal.
Fig. 8. Exterior view of clawed inner petal.
Fig. 9. Interior view of clawed inner petal.
Fig. 10. Interior view of unspurred outer petal.




OWNBEY—MONOGRAPH OF CORYDALIS

## Explanation of Plate

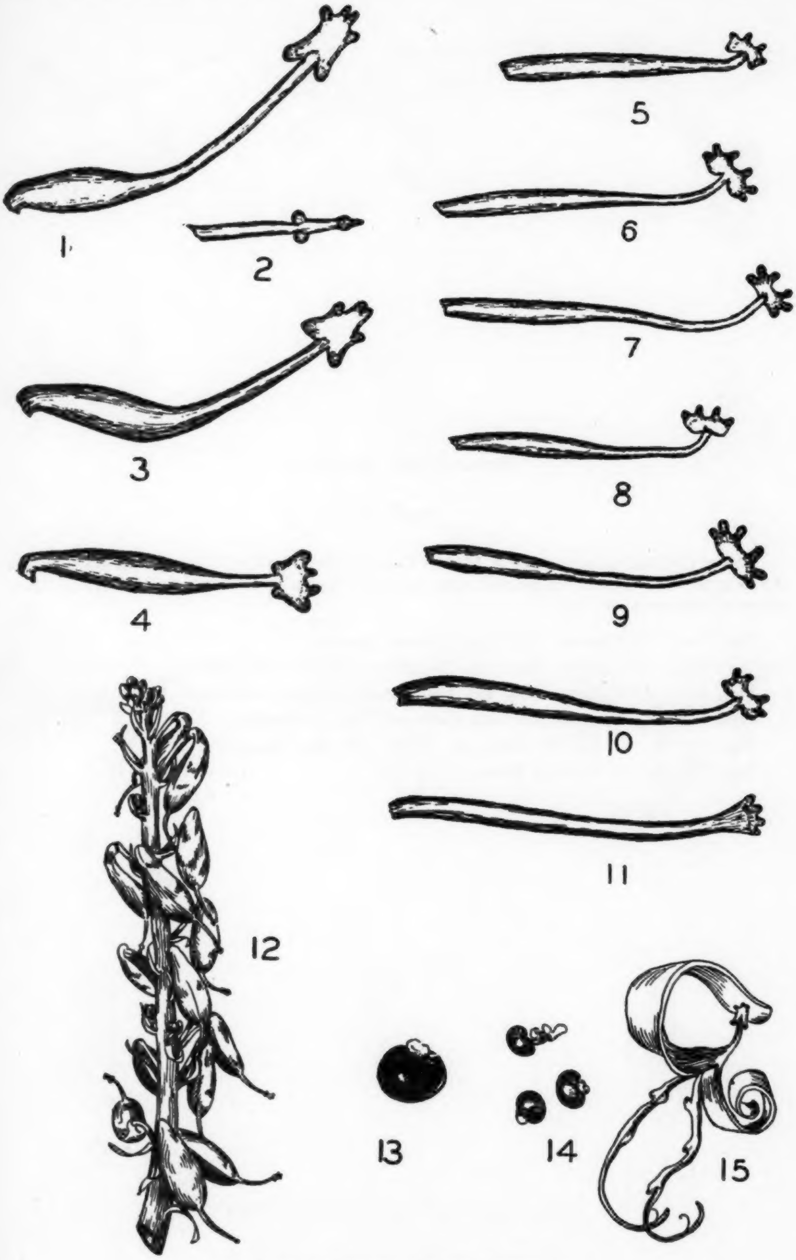
### PLATE 29

Figs. 1–11. Gynoecia of species of *Corydalis* at flowering time; drawn especially to show morphology of the stigma. Each drawing is representative of all subspecies of the species; × about 8.

Fig. 1. *C. Caseana* Gray.
Fig. 2. *C. Caseana* Gray; side view of stigma.
Fig. 3. *C. Scouleri* Hook.
Fig. 4. *C. pauciflora* (Steph.) Pers.
Fig. 5. *C. micrantha* (Engelm.) Gray.
Fig. 6. *C. curvisiliqua* Engelm.
Fig. 7. *C. aurea* Willd.
Fig. 8. *C. flavula* (Raf.) DC.
Fig. 9. *C. crystallina* Engelm.
Fig. 10. *C. pseudomicrantha* Fedde.
Fig. 11. *C. sempervirens* (L.) Pers.

Figs. 12–15. *C. Caseana* Gray; drawings representative of Sections Ramoso-sibiricae and Pes-gallinaceus.

Fig. 12. Raceme in fruit; × about 1.
Fig. 13. Seed; × 4.
Fig. 14. Seed; × 2.
Fig. 15. Fruit, showing manner of dehiscence; × 4.



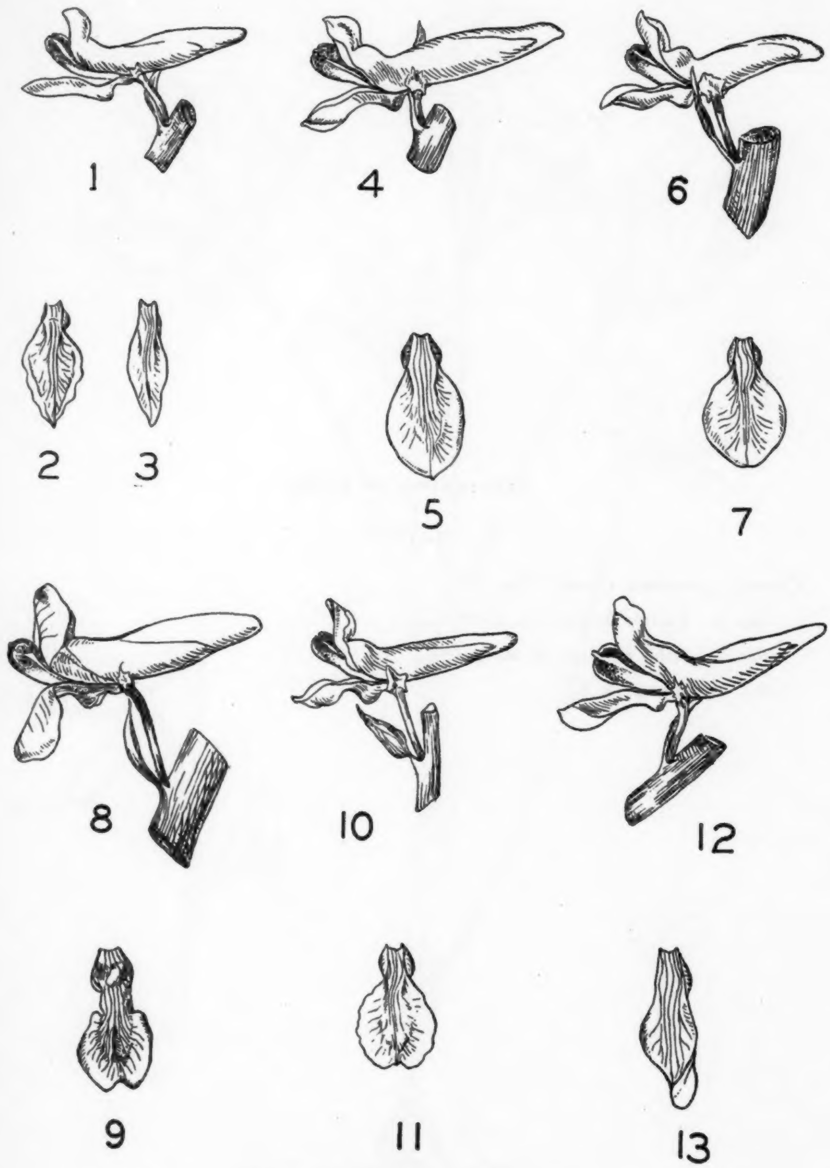

OWNBEY—MONOGRAPH OF CORYDALIS

## Explanation of Plate

### PLATE 30

Flowers of the subspecies of *Corydalis Caseana* Gray and of *Corydalis Scouleri* Hook. An interior view of the unspurred outer petal is shown in each case to illustrate differences in structure; × 1½.

Figs. 1–3. *C. Caseana* Gray ssp. *Caseana* Ownbey.
Figs. 4–5. *C. Caseana* Gray ssp. *Brandegei* (Wats.) Ownbey.
Figs. 6–7. *C. Caseana* Gray ssp. *brachycarpa* (Rydb.) Ownbey.
Figs. 8–9. *C. Caseana* Gray ssp. *Cusickii* (Wats.) Ownbey.
Figs. 10–11. *C. Caseana* Gray ssp. *hastata* (Rydb.) Ownbey.
Figs. 12–13. *C. Scouleri* Hook.




OWNBEY—MONOGRAPH OF CORYDALIS

## Explanation of Plate

### PLATE 31

*Corydalis pauciflora* (Steph.) Pers.

Fig. 1. Raceme in fruit; × about 1½.

Fig. 2. Habit of plant; × about 1½.

Fig. 3. Stigma; × 8.


OWNBEY—MONOGRAPH OF CORYDALIS

# A STUDY OF HEVEA (WITH ITS ECONOMIC ASPECTS) IN THE REPUBLIC OF PERU[1]

R. J. SEIBERT[2]

## INTRODUCTION

Natural rubber holds, and will continue to hold, a leading position among the commodities of the world. It is relatively a newcomer among the necessities of our advancing civilization, yet its absence would change the conveniences of modern life to drudgery.

Various articles made from *Hevea* were perhaps first described from the Amazon valley in 1535 by the historian Oviedo y Valdes. Two hundred years elapsed before La Condamine, during 1734-1744, brought out samples of rubber from the Amazon valley, introduced the strange material to European nobility, and later published his reports, which included a crude drawing of the *Hevea* tree. The *Hevea* rubbertree received its formal botanical treatment in 1775 by the French botanist Aublet, who described it as *Hevea guianensis* from material collected in French Guiana.

Colonial policies of rigid forign trade barriers prevented rubber from reaching the open market until after the Napoleonic invasion of Portugal. In 1823, however, the first commercial shipment of rubber reached the United States in the form of several hundred pairs of rubber shoes manufactured by the Para Indians. Stimulated by the invention of the vulcanization process by Charles Goodyear in 1839 and the great advances of the automobile industry of this century, rubber became the "gold" of the Amazon. An ever-increasing demand of a decreasing supply resulted in the decline of the Amazon jungle exploitation. Its complete collapse was brought about by the development of *Hevea* plantations in the British and Dutch East Indies, which, with their inevitable large-scale industry and consequent lower prices, rapidly took over world production during the second decade of this century. Since rubber was no longer supplied to the United States from South America, the penalty was paid during the recent war for virtual East Indian monopoly. We can appreciate, now, the efforts of our government in attempting to stimulate small farm rubber production throughout Latin America (Blandin, 1941; Klippert, 1942).

Since Aublet's first description of the genus *Hevea* in 1775, about 100 species, varieties, subspecies and forms have been described under various name combinations. Although *Hevea brasiliensis*, under cultivation, has been studied with con-

[1] An investigation carried out at the Missouri Botanical Garden in the Graduate Laboratory of the Henry Shaw School of Botany of Washington University and submitted as a thesis in partial fulfillment of the requirements for the degree of Doctor of Philosophy. Field observations and data were obtained in the course of the writer's official surveys and jungle exploration work during 1940 to 1946 as Botanist for the Division of Rubber Plant Investigations, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, United States Department of Agriculture.

[2] Botanist, Division of Rubber Plant Investigations, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture.

Issued October 31, 1947.

siderable detail, little is actually known about it, and less about the other species as they occur naturally in the Amazon valley. The majority of collections and studies have been confined to the navigable rivers, a narrow margin away from these streams, and around centers of habitation. What *Hevea* forms exist, and how they exist, between the major streams and their headwaters in the eastern Andean foothill arc that skirts the range limit of the genus, will remain a question as long as interstream areas are undeveloped. This question will furthermore remain as long as transportation is largely confined to the main waterways and until more than an occasional individual with scientific interest studies the genus, its components, and its ecology.

Through the studies of Dr. Adolfo Ducke, the great authority on Amazonian botany, and those of Drs. Richard Evans Schultes and J. T. Baldwin, Jr., we are coming to realize that the specific entities of the genus are limited to less than a dozen. These entities can be rather clearly delimited morphologically and ecologically in spite of considerable intraspecific variation. It is becoming evident that both geographic and morphological forms are being established within the species, that interspecific hybridization frequently occurs in nature, and that apparently few genetic barriers exist between the species.

With the recent war-time stimulation to wild-rubber tapping in the Amazon valley, modern advances in transportation methods, and the ever-increasing need for plant improvement programs, the Division of Rubber Plant Investigations, U. S. Department of Agriculture, has pursued basic studies of *Hevea* in its natural habitats. In addition, it has undertaken the selection of superior strains of *Hevea brasiliensis*, as well as of other species and varieties from the jungles, and established them in Tropical American experiment stations where a planned system of *Hevea* plantation improvement is under way (Brandes, 1941, 1943; Rands, 1942).

Material and data derived since 1940 from the efforts of the Department of Agriculture, in cooperation with the Latin American Republics surrounding the Amazon valley, have augmented substantially our previous knowledge of *Hevea* as a whole. With such data we can begin to visualize in an over-all manner the morphology, taxonomy, distribution and genetics of the genus preliminary to a comprehensive monographic work, though many gaps remain to be filled in all countries concerned. Moreover, we can begin to make sound progress, through selection and breeding, toward the quality of planting material, disease resistance and adaptability, as well as increasing production while lowering costs.

## Scope of the Work

This study considers the genus *Hevea* as it is known to occur in the Republic of Peru. Although I devoted three years to its study there, and others before me have collected and written of the Peruvian species, vast areas exist between the relatively few stations studied for which hear-say and assumption still must take the place of accurate information.

It has, of course, been impossible to consider the Peruvian Heveas without first taking cognizance of speciation in the adjoining Amazonian countries, particularly in Brasil. The genus, besides being of great economic importance, has the distinction of being sharply confined within the *hylaea*, or Amazon River drainage basin, except in its northeastern distribution where the range extends to the watersheds of coastal drainage basins in the Guianas and to some extent in southern Venezuela.

Speciation in *Hevea* has been considered a difficult problem and has been treated in various fashions. Because the genus is composed mostly of large trees it not only has been difficult to collect but seldom has yielded complete study material. The result has been that species often have been described solely on sterile material, only to be described later as another species on the basis of fruiting or flowering material. Comprehensive studies of comparative morphology are lacking, although there has been some study of floral morphology, particularly by Hemsley (1898). Unfortunately, natural intraspecific variation has not been given due consideration; and an amazing number of prominent and reliable specific characters have been entirely overlooked.

Much of the following discussion will deal with several newly proposed floral and vegetative characters which appear to have constant specific value and are of great practical use to both the herbarium and the field worker. That such significant characters have been overlooked previously is further evidence that constant and repeated observation has no substitute for revealing new plant features. Characters present but not previously recognized for their value, or inspirations from that subconscious feeling of "indescribable differences," under repeated observation of the unit as a whole, may loom to the conscious as significant features in the key to solution.

This paper is of necessity provisional. It will try to bear out new evidence for speciation in *Hevea* along with that known and used in the past. An attempt is made to devise a practical key to the species which may be of equal use to the herbarium and field worker. For the first time it will bring together the taxonomy of the Peruvian Heveas as a unit, as well as those of the neighboring country, Bolivia. The paper will solicit trial by those who encounter this group of plants, and, it is hoped, will stimulate further comparative morphological observations by others, so that monographic treatment of the genus may be eventually in order. It will attempt to add its bit to the promotion of cooperation between the taxonomist and the geneticist, both of whom will have a long and fertile field of research in this highly important genus of trees.

## Acknowledgments

To the Division of Rubber Plant Investigations, Bureau of Plant Industry, Soils and Agricultural Engineering, Agricultural Research Administration, U. S. Department of Agriculture, with which I have been associated as Cooperative Agent since July 1940, I am indebted for facilities and experience gained through their Plantation Hevea Improvement Program carried on in cooperation with

thirteen Latin American countries. The Division has kindly extended to me a year's leave of absence during which time it has been possible to continue my studies at the Missouri Botanical Garden.

Material for much of this paper was gathered from the Republic of Peru. I am deeply grateful for aid rendered by government officials concerned with the rubber program in that country. The Estación Experimental Agrícola de Tingo Maria, Peru, a cooperative agricultural experiment station maintained by the Office of Foreign Agricultural Relations, U. S. Department of Agriculture, and the Peruvian Ministry of Agriculture through its Peruvian and United States employees, was of constant aid in propagating and maintaining living material of jungle selections. To the many rubber tappers, *shiringeros* (Seibert, 1947), with whom I worked and lived, must go much credit. They are the men who help one in the "bush" when help is most needed. They are the men who know rubbertrees instinctively, and from them came many basic facts which we in return can put into scientific language.

Preparation of this paper has meant the amassing of most of the *Hevea* specimens from the major herbaria of the United States, namely, U. S. National Herbarium, New York Botanical Garden, Chicago Natural History Museum, Missouri Botanical Garden[1], Gray Herbarium, Arnold Arboretum, and the National Arboretum, to the curators of which I am indebted for loaned material.

Dr. John T. Baldwin, Jr., and Dr. Richard Evans Schultes, both of whom are actively concerned with somewhat similar studies in other Amazonian countries, have made available to me their collections of *Hevea*. They have been most considerate and helpful in discussions, both verbally and through correspondence, and have tested for me a number of morphological characters here proposed. Mr. Hans Sorensen, Agent, Rubber Plant Investigations, stationed at the Instituto Agronomico del Norte, Belem, Brasil, has kindly tested and confirmed my observations regarding the question of short-shoots. Dr. John B. Carpenter, Agent, Rubber Plant Investigations, stationed at the Estación Experimental Agricola de Tingo Maria, Peru, very kindly has forwarded to me herbarium speceimens of critical material from my living jungle selections as they have come into flower since my departure from Peru. To these institutions and individuals and to many others who have been of aid in this phase of the Hevea Improvement program, I wish to express my appreciation for the fine spirit of whole-hearted cooperation which is so much needed in coordinating large-scale programs of national and international extent.

## Morphology of the Genus

*Habit.*—

Without exception the genus is woody. For the most part it is composed of medium-sized to large trees, which in *Hevea guianensis* var. *lutea* and especially *H. brasiliensis*, frequently may reach 45 meters in height under most favorable growing conditions. Largest trunk diameters are found within *H. brasiliensis*, and in Madre de Dios, Peru, it is not uncommon to find trees 1 meter, occasionally 1.5

[1]To Dr. Robert E. Woodson, Jr., I am indebted for valuable guidance of the research and presentation of the morphologic and taxonomic aspects of this paper.

meters, in diameter at 1 meter above the ground.

In contrast to the large trees of the genus, two entities have been reported in which the habit is low and shrubby. The case of *H. camporum* Ducke (1925), collected by R. Monteiro da Costa in the *campinas*[2] between the headwaters of the rivers Manicore and Marmellos, southern tributaries of the lower Madeira, is very poorly understood because of sparse herbarium material collected. The region from which it comes apparently is hilly, semi-open, grassy and scrub-forest land, unfavorable to good tree growth. According to Ducke (Schultes, 1945) the species perhaps is only a dwarf form of *H. pauciflora* var. *coriacea.*

The other interesting case of dwarfed or shrubby habit in the genus is *Hevea nitida* var. *toxicodendroides* (Schultes, 1947), discussed by Schultes (1944) and described as *H. viridis* var. *toxicodendroides* Schultes & Vinton. This variety was discovered in Colombia from the upper Apapores Basin, growing on and around apparently old sandstone outcrops of at least Triassic age, on which semi-xerophytic conditions exist. These plants are about 12 feet tall and are quite bushy or shrubby in aspect. Otherwise they resemble the species in morphology and size of the leaves, flowers, fruit and seed. Thus it appears that variation may be more ecological than morphological. Experimental growing only can determine this.

From apparent intergradations between the normal type of tree branching and the low branching of the shrubby types one may observe and interpret conditions frequently encountered in plantations of the commercially grown *H. brasiliensis.* Pruning is a common practice and certain "clones"[3] under normal conditions tend to form a low branching habit. It is necessary, through pruning, to prevent the formation of such low branches as it would interfere with a good tapping panel. Under conditions of undue drought and where soil is not suitable for growth of *H. brasiliensis* almost all individuals of the species will tend to have profuse and low-branching habits, not at all typical of the same plants growing under natural conditions.

*Trunk.—*

Growing under flooded conditions, where the trees stand in various depths of water for nearly the entire year as do *H. Spruceana, Benthamiana* and *microphylla*[4], the trunks are distinctly swollen toward the base. This "bellying" is pointedly referred to by the Brasilian name for *H. Spruceana, seringueira barriguda*[5]. The amount of bellying and the height to which it extends may possibly be some indication as to how high flood waters reach up the trunk. Above the uniformly swollen portion, the trunk suddenly tapers upward. A graphic example of this bellying effect due to flooding appears to be well illustrated by contrasting the *H. brasiliensis* of the periodically inundated land, *tierra baja*[6] of the upper Amazon proper,

[2]*Campinas* in Brasil refer to grassy, scrub-forest hilltop land.

[3]A clone in *Hevea* plantation terminology refers to an individual tree which is vegetatively propagated through successive generations by means of bud-grafting.

[4]Schultes ('47) has shown from type studies at Kew that *H. minor*, as at present known, should be referred to *H. microphylla.*

[5]*Seringueira barriguda* in Portuguese means big-bellied rubbertree.

[6]*Tierra baja* in Peru refers to low inundated land along rivers; and *tierra altura* to land above the level of river flooding.

with that growing on well-drained *tierra altura* of Pando in Bolivia and Madre de Dios in Peru. Wherever the trees are subjected to periodic inundation the swollen bases are conspicuous and rather suddenly tapering several feet above the ground. On *tierra altura* the trunks are definitely cylindrical with no more than the normal gradual tapering in girth.

The normal trunk for the species growing on well-drained land is cylindrical to the ground level with a very slight tapering or girth decrease upward. Under usual forest conditions the first branches depart from the upper third of the tree. It is not uncommon to find forest giants with 90 to 100 feet of cylindrical trunk to the first branches.

There appears to be no reference to, nor have I seen any cases of buttressing. However, Dr. Baldwin informs me that he found a buttressed tree on the Rio Negro, which he is inclined to feel resulted through intergeneric hybridization with *Cunuria*. It would appear that buttressing is not a characteristic of *Hevea*.

Interesting evidence concerning the age of *H. brasiliensis* trees from Bolivia and the Acre Territory of Brasil is given by La Rue (1926). These areas and that of adjoining Madre de Dios, Peru, are characterized by having one distinct rainy and one distinct dry season per year, conducive to the formation of annual tree rings. Although no increment borer was available, I was able to observe the trunks of a number of trees at Iberia, Peru, which were felled to make way for an air strip. Annual rings were not noticeable until nearly a year after felling, when partial decomposition of the wood had set in. A radial cross-section of one of these trees, 84 cm. in diameter, showed 211 annual rings. There is indeed little doubt that some of the largest forest giants were already growing before the discovery of America.

*Bark*.—True outer bark color and other characteristics in *Hevea* are often distinctively overshadowed by the predominance of crustaceous lichens which makes the trees easily spotted in the forest. As yet there has been insufficient investigation and description of the bark as applied to specific delimitation. In general, it is quite smooth with some scaling and color range from light gray to dark brown. There appears to be much intraspecific variation in bark characters, ranging through very smooth, pustuled, flaky, shaggy, to definitely corky within *H. brasiliensis* itself. An extreme has been described by Bartlett (1927) as *H. brasiliensis* mut. *Granthami*. Bark variants of this and many other types occur not only in plantation material but in the wild as well, together with the intergrading forms. Schultes (1945) reports evidence from Colombia that bark variations are of importance in distinguishing subspecific variants in *Hevea*. These bark variants are important factors in a selection of trees for plantation use, in that ease of tapping may be considerably hampered by such rough strains. Outer bark variations would appear to be of considerable use in clone distinction (Frey-Wyssling, 1933).

The inner portion of the bark, or phloem, is, from the economic standpoint, the important part of the tree anatomy, since the latex vessels located here furnish the natural rubber of commerce when cut in the process known as "tapping."

Here again there may be as much or seemingly more intraspecific as interspecific variation. Within *H. brasiliensis* the phloem of mature trees may vary in thickness from about 0.5 cm. to about 2 cm. Apparently, due to the cambial development of concentric rings of phloem, the latex vessels occur in concentric rows, the number of which is highly variable, ranging from about 8 to 35. There would seem to be no correlation between number of latex rows, their individual size or productivity, and age or size of the mature tree. Perhaps one of the most striking variations in phloem is the color. This variation, or series of variations, for *H. brasiliensis* appears to reach its maximum toward the southwestern and western part of the species range. Observations of thousands of trees seemingly have shown all range of variation through tan, brick, purplish red, reddish purple and blackish purple. La Rue (1926) has a considerable discussion of these color variations. There is a feeling among the rubber tappers that the trees with purplish phloem, and particularly those with the *preta*[7] or blackish purple color, give the best yield and the superior quality of rubber. Although there may be such a tendency, this color is by no means a constant criterion as evidenced from jungle selection work carried on in the Madre de Dios area.

Texture of the phloem likewise is variable, ranging from very hard, with high number of stone cells, and difficult tapping, to soft, easy-cutting, almost "cheesey" texture. There seemingly is a tendency for trees with purplish phloem to have a softer texture than those with more tannish phloem. It is interesting to note that though a tree may have virgin bark of a tannish or light-colored phloem, the renewed phloem from previously tapped portions of the same tree has a reddish or purplish color. Trees with a reddish or purplish virgin phloem, as well as those with renewed secondary reddish or purplish phloem which is tan in virgin condition, often exude a reddish or purplish dye-like fluid independent of the latex flow when freshly cut.

With the exception of the seemingly complete absence of so-called *preta* trees from the lower Amazon region, there would seem to be no geographic, ecologic or edaphic range limitations of these various bark variations. Any randomly selected *estrada*[8] from the Madre de Dios may contain a fairly complete range of color and other bark variations within close proximity. There furthermore is no conclusive evidence from the Madre de Dios region that any of the numerous bark variations are constantly associated with such intraspecific morphological variations as leaf size and shape.

Although little is known of bark variations in other species than *H. brasiliensis*, it appears that similar variations exist in *H. guianensis* var. *lutea*. Here the outer bark also shows variations in type and amount of scaling. The phloem color ap-

[7] *Preta*, meaning black in Portuguese, is used to describe trees of *H. brasiliensis* in which the phloem is distinctly blackish purple in color.

[8] An *estrada* consists of about 100 to 150 rubber trees, joined one to another by a forest trail running from and returning to the *shiringero's* house in somewhat loop fashion. A map of an estrada has been excellently figured by Preusse-Sperber (1916). The rubber tapper is usually assigned two estradas, the trees of each being tapped on alternate days.

pears to vary from light tan to a somewhat purplish red. The texture and thickness also are quite variable.

*Latex.*—Slight chemical differences distinguish the rubber from the latex of the different species. Great differences, however, do occur when the latex as a whole, including its serum and non-rubber content, is taken into consideration (Parkin, 1900). It is well known that *H. brasiliensis* as a species gives the most abundant yield and the best quality of rubber from the manufacturing standpoint, while *H. Benthamiana* probably ranks second. It is also true, but less well known, that in the species *H. brasiliensis*, within areas of its distribution as well as between its regions of distribution, there are great variations in these qualities. On the basis of these facts, large-scale selection and later breeding programs in the Far East have been able to step up yields per acre from less than 450 pounds annually to recent experimental yields as high as 2000 pounds. Such has been done from the original stock of less than 100 trees of *H. brasiliensis*[9] finally surviving from those introduced by Henry Wickham into Ceylon and Singapore from seed he collected near Boim, Rio Tapajoz, Brasil. From this might be visualized ultimate yield possibilities by choosing stock from such areas in the southwesternmost limits of *H. brasiliensis*, as in the Madre de Dios, where average tree yields are proving to be some three times as great as the region from which the Far Eastern stock was obtained.

Although *H. guianensis* and its varieties may be characterized partially as having yellow latex and considered as having low yields of weak rubber, there is a great deal of tree to tree and area to area variation. It is usually noted within this group that the color of the latex may become nearly white after successive tapping over periods of time. Latex color appears to be no criterion of quality inasmuch as both *H. brasiliensis* and *H. Spruceana* are characterized by white latex. The former species produces excellent quality and the latter very inferior quality shunned by all rubber tappers. Cases of latex reaching sulphur-yellow tones are known to exist in *H. brasiliensis*, both among plantation-developed clones and among jungle trees. There is no evidence that such individuals produce inferior rubbers. Trees have frequently been found in the jungle selection work where the latex of the young branches is yellow, while that from the trunk is perfectly white.

Cases are known where the latex is very high in resin content, producing a very "tacky"[10] rubber. Such occurrences are frequent in areas below Iquitos where apparently introgression of *H. pauciflora* into the *H. guianensis* complex has resulted in the weakening of the rubber to such an extent that freshly coagulated rubber fails to keep its shape even over night. *H. pauciflora* itself has a very poor resiny rubber and never is tapped commercially. Allen *(No. 3298)* reports a

---

[9] According to Mann (1940), "It seemed fairly clear, however, that the whole of the rubber in Malaya originally came from 27 seedlings of the original Wickham collection that went to Singapore in 1876."

[10] "Tacky" rubber is that which in coagulated form remains resiny and sticky, refusing to maintain its original shape. It is usually very weak with little elasticity.

collection of *H. nitida* from the Vaupes region of Colombia, in which adulteration of the latex with that of good latex from other species resulted in the ruining of all the latex, even preventing proper coagulation.

Latex yield, and often its color and quality, cannot be gauged from the first incision made into the tree. Both plantation and jungle tappers have found that the normal tree is stimulated by what is termed "wound response"[11] under systematic tapping. Yields from the individual tree increase as much as 20 per cent after several tappings or even several weeks of tapping, and so long as regular systematic tapping is carried on this optimum yield is obtained. On the other hand, rare cases have been seen in which the tree gradually "drys"[12] by the same system.

Latex flow from tapped trees is, of course, affected to some extent by the water content of the latex. Individual trees in the same jungle area will show considerable normal deviation from the accepted average of about 30–33 per cent Dry Rubber Content (DRC) and appear to range from between 20 per cent to as high as 45 per cent DRC. Seasonal variations also occur and lag somewhat in direct proportion to the amount of rainfall. A climate with a more or less uniform rainfall throughout the year and with no long pronounced dry season would be necessary if year-around tapping were desired. A further factor affecting latex flow, and one which is poorly understood, seems to be related to temperature and time of day at which tapping is done. Plantation experiments appear to have proved that flow and yield are substantially larger if tapping is done very early in the morning, before the sun reaches its full effect, or before 10:00 a. m. Furthermore, on cloudy days the time of maximum flow is extended considerably. Similar effects have been observed by the jungle tappers and apparently is in part directly responsible for the custom of many tappers to rise as early as an hour or two before sun-up and start their work with the aid of a lantern. During abnormal periods of cold weather in the upper Amazon regions[13] it also has been observed that tree yields considerably increase above normal.

*Branch system.*—

The normal branch system of the genus is composed of the prominent erect main axis from which arises a symmetrical system of secondary branches. Under usual forest conditions branching is found on the upper one-half to one-third of

[11] "Wound response" (Royal Botanic Garden, Ceylon, 1899) is the plantation term given to the normal increase in a tree's yield induced by systematic regular tapping over a period of days or weeks, from the comparatively low first-tapping yield to the normal yield of the same tree after it is in regular tapping.

[12] It is frequently convenient, when speaking of *Hevea* trees, to use the terminology of the dairy industry. To go "dry" is one of those terms.

[13] A rather broad area of the upper Amazon valley, roughly between Porto Velho and the Andean foothills, is subject to yearly cold periods lasting about 2–3 days known in Brasil as *friagem* and in Peru variously as *friaje* or *varaza*. One or more of these periods usually occurs around the months of July or August during which time strong southeast winds, recorded at Maldonado as high as 100 mph., precede a driving rain of short duration. This is followed by lighter winds, cloudy weather and temperatures as low as 10° C.

the tree. Radical exceptions to this form occur in *H. camporum* and *H. nitida* var. *toxicodendroides* which are characterized by low shrubby forms. Wind damage to forest trees, as well as artificial topping or pollarding occasionally practiced in plantations, appears to have similar effects in stimulating strong lateral branch development. There also would seem to be inherent branch differences among individuals or strains of the same species.

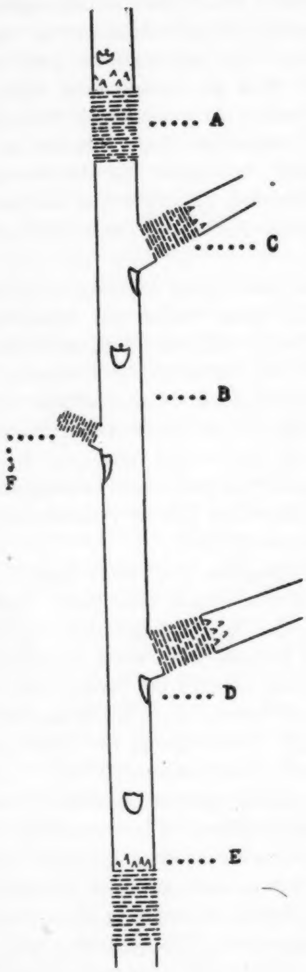
Two major habital forms within *H. brasiliensis* may be observed: (1) possibly the typical form in which there is a prominent main axis with small lateral branches; and (2) the form with lateral branches as prominent as the central axis and frequently even replacing it. Although plantation material appears to be largely of the latter type, representatives of the former also occur. Seed progeny from the low-river areas, as Belem and Rio Tapajos, as well as from such up-river areas as Acre, Madre de Dios and Iquitos, all growing at the Estación Experimental Agrícola de Tingo Maria, show both types of branching and intermediates to exist from all areas. There is a tendency, however, for the latter type to predominate in progeny from low-river areas, while the former appears to be predominant in up-river areas.

Another branch variation, discussed with reference to clonal differentiation by Frey-Wyssling (1933), concerns the angle and form at which the lateral branches arise from the main axis, being from nearly vertical to nearly horizontal. Until we have more information from both natural and cultivated habitats for all of the species, branching habits would seem to be primarily intraspecific variations and of more use in clonal than in specific delimitation.

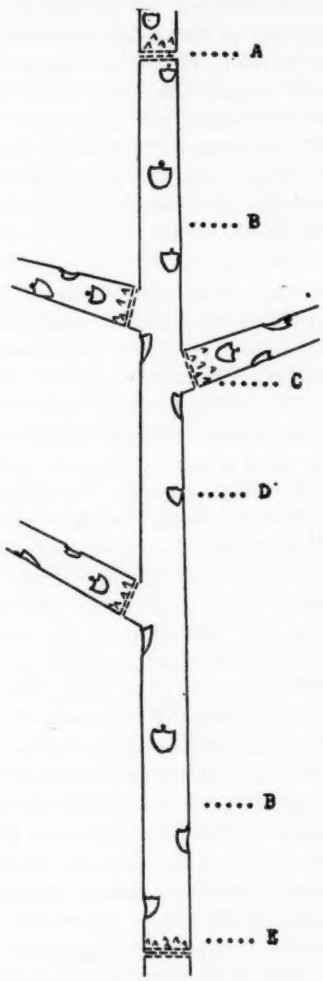
*Roots.*—

With the exception of *H. brasiliensis,* and to some extent *H. guianensis* with its variety *lutea* and *H. Spruceana,* little is known of the *Hevea* root system. A long, prominent tap root seems to be the rule, and also that rather prominent laterals radiate out from just below the ground surface to form a surface-feeding network. Under certain cultivated conditions, such as are found at Bayeux, Haiti, where a permanent high water table lies one and a half to three feet from the surface, the long tap root of *H. brasiliensis* either branches profusely at the water table or suddenly turns and follows parallel with it. In the Madre de Dios region where the species grow naturally on well-drained land, the root system is as found under normal plantation conditions. In the Iquitos area, where the species naturally grow part of the year in several feet of water and the rest of the year with a comparatively low-water table, the roots of several trees, uprooted by high winds, also have been found to be of the normal type. I know of no reference to the root systems of such species as *H. Benthamiana, microphylla* and *Spruceana,* which naturally grow permanently in water. *H. Spruceana,* however, does react normally in its root development when planted on well-drained land.

*Long-shoots and short-shoots (Flushes and Interflushes):* The genus *Hevea* is characterized by periodic (annual except in seedling stage), rapid stem growth or elongation alternating with a long period during which stem elongation




Text-fig. 1. Leafy shoots (flushes) alternating with relatively elongate caducous-scaly short-shoots (interflush short-shoots): A—conspicuous interflush short-shoot; B—long-shoot or flush; C—lateral branch development from a short-shoot or spur; D—leaf-scar; E—leaf scales on lower part of flush adjoining the short-shoot; F—lateral spur development.




Text-fig. 2. Leafy shoots (flushes) alternating with narrow rings of bud-scale scars (interflush rings): A—inconspicuous interflush short-shoot; B—long-shoot or flush; C—lateral branch development from an inconspicuous short-shoot; D—leaf scar; E—leaf scales on lower part of flush adjoining the interflush ring; lateral spur development inconspicuous.

and leaf formation are arrested or reduced. These intervals of rapid stem development or long-shoots have been referred to in plantation use as "stories" (Frey-Wyssling, Heusser & Ostendorf, 1932) and perhaps more popularly as "flushes" (Assoc. Cent. Exp. Sta., 1939). With the exception of noting the presence of terminal bud scars, and of scale buds at the area between "flushes," the center of the "corona"[14] region in budding terminology, little attention has been paid to this character in specific determination. It appears that the interval between flushes, or terminal bud scar region (text-fig. 1), might best be known as the "interflush" which, perhaps, is referable morphologically to a "short-shoot" (pl. 32, fig. 2).

No literature has yet come to my attention making any reference to one of the most striking morphological characters in the genus *Hevea*—the "short-shoot." The short-shoot, or spur, is well known in *Ginkgo* (Collins, 1903) and a number of conifers (Chamberlain, 1935). Short-shoots occur in the rosaceous fruit trees. They would appear to occur on the underground rhizomes of *Poa* and perhaps other grasses including Bamboo (note figs. 23 & 123 in Arber, 1934) and may be found in some of the higher plants, both tropical and temperate. It would not be hard to presume that a comprehensive study of short-shoots throughout the plant kingdom not only would furnish an interesting field of research, but also might lead to important taxonomic and evolutionary data.

Short-shoots generally have been given attention only when they develop prominent lateral spurs. They may continue for several years before suddenly changing their growth nature by transformation into a long-shoot. However, close examination shows that they may, and frequently do, occur terminally on the main axis and later are seen to be alternating between two long-shoots. Due to much compression of the internodes on these shoots, the normal long-shoot leaf phyllotaxy superficially appears to be changed. Furthermore, the leaves arising from these short-shoots are not entirely normal (Chamberlain, 1935).

In collecting *Hevea* for the herbarium, branching specimens are seldom chosen for the press. Thus little evidence of the presence of spurs is ever presented to the herbarium worker. In *Hevea* the short-shoots are not prone to linger for several years before developing into a long-shoot, though such has been seen on rare occasions. Ducke (1935) apparently came close to recognizing their presence, when, in his description of *H. guianensis,* he remarked: "Old branchlets with persistent scales at the terminal bud," and with regard to *H. Spruceana* pointed out "the numerous pointed scales which cover the vegetative buds."

Since, in the plantation, only *H. brasiliensis* has been under critical observation, and since short-shoots are so condensed (text-fig. 2) in this species as to be represented by little more than a narrow ring of a few scale bud scars between flushes (pl. 32, fig. 1), the character for the genus as a whole has not come into recognition. Even the classic work of Parkin (1904) on nectiferous and non-nectiferous

[14]"Corona" is a term being adopted by the U. S. Department of Agriculture to the area of the stem on which the buds are most crowded together.

bud scales fails to recognize the presence of the short-shoot. Furthermore, in the nursery where close observation might well bring out such a feature, we find that young *Hevea* seedlings and buddings have somewhat different vegetative habits from older trees. The young plant sends out a new vegetative flush barely after the previous one has matured. All the leaves from several flushes are persistent, whereas after the tree reaches about three years of age it will normally send out only one flush per year and that only after defoliation of the previous one, as in the case of *H. brasiliensis*. It is only after growth-habit maturity has been attained that the species showing distinct short-shoots will develop the character. We have a rather parallel condition in *Ginkgo* where the young plant develops only long-shoots until after it has reached some size.

The length of the flushes appears to be quite variable from year to year, probably depending both upon climatic conditions and upon the amount of shading the branch has received from other branches. From this standpoint the short-shoots of any one species appear to be less variable in length by comparison. As yet no instance has been seen where the short-shoot grades imperceptibly into the long-shoot.

The short-shoot in *Hevea* makes its terminal (and axillary) appearance during the maturation period of the flush and reaches conspicuous proportions just before the appearance of the inflorescence (pl. 33, fig. 1). In the species where the short-shoot is pronounced (*H. guianensis, Spruceana, pauciflora, rigidifolia* and *nitida*) it consists of a segment about 1 cm. long (pl. 32, fig. 2; pl. 33, figs. 2-3) covered with caducous scales (pl. 33, fig. 1-2) which morphologically are reduced leaves (Frey-Wyssling, Heusser and Ostendorf, 1932). The nodes of this portion of the stem are much compacted and number as many as 100, with internodes naturally being obsolete. The first branches of the inflorescence seem to arise from the axils of the uppermost scales (pl. 33, fig. 2) and shortly may be followed by the appearance of the young long-shoot or flush carrying the leaves. Frequently inflorescence branches also arise from the axils of the lowermost leaves of the long-shoot. On the older portions of the stem these short-shoots alternate with the long-shoots and are conspicuous at the interflush regions (pl. 33, fig. 3).

In those species where the short-shoot is much condensed or inconspicuous (*H. brasiliensis, microphylla* and *Benthamiana*—pl. 32, fig. 1), one not familiar with the genus as a whole might have difficulty in recognizing it as such. Nevertheless, the short-shoot is morphologically the same as in the previous group except that the scales or reduced leaves are very few and can be recognized at the interflush areas of the older stems as only a narrow ring of few bud-scale scars.

Cases of both natural and artificial hybridization between species of contrasting short-shoot condition, as *H. brasiliensis* × *Spruceana, H. Benthamiana* × *guianensis, H. brasiliensis* × *pauciflora*, etc., appear to show the conspicuous short-shoot, indicating its probable dominance as a factor in contrast to its opposite extreme in which the short-shoot is represented by an inconspicuous narrow ring of bud-scale

scars. Hybrids frequently appear which closely resemble the species except for having the conspicuous short-shoot. Such cases must be borne in mind when occasional specimens of *H. Benthamiana* varieties, for example, refuse proper placement in the proposed taxonomic key.

This conspicuously contrasting character is considered here as being of key significance in dividing the genus as a whole into two groups. Whether or not these two groups are entirely natural has not yet been determined; in fact, in combined consideration with many floral characters they do not appear to be entirely natural. Nevertheless, these divisions seem to be of more practical importance than previous ones based on anther number and anther whorls. It is hoped that further detailed study may be given to the question of short-shoots by others engaged in *Hevea* field work.

*Leaves.*—

The general structure of the leaf is uniform throughout the genus, being digitately 3-foliolate with the leaflets joined to the relatively long petiole by noticeable petiolules. A small, lateral, early caducous stipule is found on the stem at each side of the petiole base. Although 3 leaflets are the rule, 1, 2, 4 or 5 leaflets, or two of the leaflets grown together in varying degrees, may be found on rare occasions (Frey-Wyssling, 1931). Such abnormalities are found in both the plantation and jungle where either an occasional leaf may be abnormal or many of the leaves from the same tree show such conditions. Seedling leaves, so far as I have been able to observe, likewise normally are 3-foliolate. When leaf abnormalities do occur there seems to be a stronger tendency for the production of more than 3, rather than fewer leaflets. Conspicuous glands, or extra floral nectaries, which normally occur on the upper surface of the petiole just below the junction of the 3 petiolules, are apt to be extremely variable even on the same tree. It is from these petiolar glands that extra leaflets appear to be derived, and they may or may not be of stipular origin.

Phyllotaxy has been determined for *H. brasiliensis* (Ostendorf and Ramaer, 1931). Leaves are spirally disposed on the flushes and diverge at an angle usually of 138° (2/5) or occasionally at 103° (2/7). This appears to be the extent of variability throughout the genus. Some deviation from this might be expected in the bud scales or on the short-shoots of other species. A comparative study from fresh material will be undertaken at a later date in connection with a thorough consideration of the short-shoot within the genus.

Frey-Wyssling, Heusser, and Ostendorf (1932) have discussed in detail the tremendous variations of all parts of the leaf in *H. brasiliensis*. Observations on both field and herbarium specimens of other species indicate considerable intraspecific leaf variation to be characteristic throughout the genus. With some striking exceptions, which will be pointed out in the following paragraphs, leaves hold greater significance and consistency in distinguishing individuals or clones than for specific distinction.

*Leaf persistence:* Those who have observed *Hevea* growing, both in the plantation and in the Amazon valley, are familiar with the deciduous wintering habit of *H. brasiliensis*. During or near the end of the dry season it "winters" by losing all the leaves of the most recent flush and going through a dormant period of several weeks. The dormant period is followed by the appearance of inflorescences and, immediately after, the rapid growth of the new vegetative flush (pl. 34, fig. 1).

Under jungle conditions in any limited region, the trees of *H. brasiliensis* usually go through these stages at the same time, any one tree not lagging or being advanced by more than a few days. Under plantation conditions, particularly where there is no pronounced dry season or in abnormal latitudes or altitudes, the leaf-shed and flowering seasons may vary several months from tree to tree. In some extreme cases the same tree may be in several stages at the same time. Some branches may be defoliating and resting, others sending out inflorescences and young flushes, while still others may have mature vegetative flushes and already maturing fruit. Yet, so far as I am aware, within *H. brasiliensis*, the previous flush always defoliates completely before the appearance of the inflorescence on that particular branch. It is said that a few oriental clones[15] tend to hold their leaves while flowering, but the details are not clear to me. I am of the opinion that the actual branch which is flowering has defoliated; or, it may be that the clone is not genetically pure for the species. Such instances have been observed at Tingo Maria and Iquitos where individuals of Iquitos origin (referable to *H. brasiliensis* but very likely carrying genes of another species) hold a few leaves on the previous flush while flowering.

It should be explained that plants up to about three years of age do not show this seasonal wintering. They normally send out new flushes regularly every month to six weeks. During this stage of growth, leaves of about the top three flushes persist while those on the lower ones gradually absciss. The transition from this habit to the mature growth habit is sharp. At the proper age and size the young plant undergoes complete defoliation and continues thereafter to send out yearly flushes which completely defoliate before the appearance of the next flush.

There is good reason to believe that the *H. brasiliensis* type of defoliation and wintering does not occur in all species of the genus. No information on the subject appears to be recorded, and detailed field study of the flush and inflorescence habits of the genus as a whole is wanting.

The contrasting condition seems to exist in which leaves of mature tree flushes are persistent until well after the appearance of the inflorescence, its maturation and the presence of the new flush (pl. 33, figs. 2-3; pl. 34, fig. 2). It is not clear what, if any relationship exists between interflush rings and interflush short-shoots and the degree of dormancy. Unfortunately, insufficient field evidence is available

[15]Oriental clones are those developed and selected from cultivated *Hevea brasiliensis* growing on Far Eastern plantations.

to draw final conclusions, particularly from cultivated conditions where all the species are growing together in the same climate and soil. Mostly from evidence of herbarium specimens, the following categories appear to be evident with reference to the various species:

1. Leaves persistent on the previous year's flush until well after the appearance of the inflorescence or its maturation.
   *H. Spruceana*—From the specimens it seems that the new flush is very slow in appearing after the inflorescence and that the fruit may be well along in its development before the new flush appears. Meanwhile, the previous flush leaves are very persistent. All inflorescence branches arise from the axils of the scales on the short-shoot (pl. 33, fig. 2).
   *H. rigidifolia*—The previous flush leaves are very persistent until well after inflorescence maturation. From the few specimens at hand it is not possible to determine how long after inflorescence maturation the new flush makes its appearance. As above, all inflorescence branches arise from the short-shoot scale axils.
   *H. pauciflora*—The previous flush leaves show a very strong tendency to persist until after the appearance and maturation of the inflorescence, as well as the appearance of the new flush which follows almost immediately after that of the inflorescence. Most of the inflorescence branches arise from the short-shoot scale axils but some may arise from the axils of the lower leaves on the new flush. A few specimens show a tendency for defoliation at the time the new flush makes its appearance. This may be due partly to removal of excess leaves by the collector (a frequent bad practice to "improve" the herbarium specimen) or it may be partly due to frequent hybridization with other species. The study of these characters in living material is especially critical in the *H. pauciflora* complex.
   *H. guianensis* and varieties—A stronger tendency is shown for defoliation or partial defoliation preceding the appearance of the inflorescence than in *H. pauciflora*. Nevertheless, the majority of the specimens show at least a few leaves, particularly upper ones, remaining at the time the inflorescence appears and until the appearance of the new flush which shortly follows. Most inflorescence branches arise from the short-shoot scale axils. However, as in *H. pauciflora*, the upper inflorescence branches tend to arise from the axils of the lower leaves of the new flush.
   *H. nitida*—This species is so very poorly represented in flowering material that little can be said except that some previous year's flush leaves (upper) tend to persist until after the appearance of the inflorescence. Although the basal inflorescence branches arise from the upper short-shoot scale axils, a greater number of the upper inflorescence branches arise from the leaf axils on the lower half of the flush.
2. Leaves not persistent on the previous year's flush, *i. e.* they absciss before the appearance of the inflorescence on that branch.
   *H. Benthamiana*—Leaves are completely abscissed before the appearance of the inflorescence. The flush immediately follows the appearance of the inflorescence. The basal inflorescence branches arise from the uppermost bud-scale axils but mostly from the axils of the leaves on the lower two-thirds of the flush. A number of specimens, superficially resembling *H. Benthamiana*, show some persistent leaves, but close examination of the leaf, shoot and flower gives ample evidence that the specimens represent hybrids between *H. Benthamiana* and *H. pauciflora*, *guianensis* var. *lutea*, or *Spruceana*, from which the persistent leaf character probably is derived.
   *H. microphylla*—Leaves are completely abscissed before the appearance of the inflorescence. Lower inflorescence branches arise from the upper bud-scale axils while the rest arise from the leaf axils of the lower third of the flush. However, on account of lack of sufficient material, the above observation may be somewhat inaccurate.
   *H. brasiliensis*—Leaves are completely abscissed before inflorescence appearance. Lowermost inflorescence branches arise from the lowermost scale leaves of the flush and continue to arise from the axils of nearly all leaves of the flush except from a few of the uppermost ones[16].

---

[16]The fact that most axillary buds of the flush leaves have developed inflorescence branches may be of importance when it is necessary to bud graft material from the branches of mature trees. If such budding be necessary, as it is in selecting jungle trees for experimental and plantation use, one should choose so-called "corona" buds, those which occur in a rather crowded position near the terminus of the flush and from the inconspicuous short-shoot where no inflorescence branches likely have arisen.

It perhaps is of importance to note that the species falling in the first category showing persistent leaves are also those considered to have conspicuous short-shoots. Those of the second category with non-persistent leaves coincide with those species without conspicuous short-shoots. Although the character is used to a limited extent in the proposed key, I cannot as yet place full emphasis on it until further study has been made from living plants.

*Leaflets:* In a consideration of leaf characters as an aid to distinction of the various species one is forced to choose carefully and even then some overlapping can be expected. Although *Hevea* specimens usually are very large and difficult to collect, some leaflets may be found on the ground beneath the trees at any season. It is important, then, that we be able to derive maximum specific use from even a fallen, disintegrating leaflet and the aid of a pair of field glasses in determining an uncollectable forest giant from some area where *Hevea* has perhaps previously not been collected.

Position: Position of the mature leaflets with reference to the petiole axis is of prime importance in associating a particular plant within certain groups of species.[17] Two distinct contrasts may be found, *i. e.*: (1) Leaflets erect to slightly horizontal, in which case they stand up above the axis of the petiole to which they are attached. This type of position is found in the *H. guianensis* complex. (2) Leaflets distinctly horizontal to reclinate, the leaflets standing out in a plane parallel to that of the petiole or hanging down nearly perpendicular to the petiole axis. *Hevea brasiliensis* and *H. rigidifolia* are typified by reclinate leaflets while the remaining species are rather intermediate between horizontal and reclinate.

Lower lepidote surfaces: *H. nitida* is the only species in which scales are lacking or, at most, extremely sparse and sufficiently microscopic to produce a strikingly concolorous leaflet. All other species are characterized by having varying densities of minute, whitish, epidermal scales distinguishable with a strong hand lens. The presence of these scales accounts for the characteristic dull lustre and occasional whitish color of the lower surface. The scales are most densely disposed on the mature leaflets of *H. rigidifolia* and *H. pauciflora,* where they lie one against the other in tile-like regularity and are noticeably angular (hexagonal) in outline. In *H. Benthamiana* they are quite densely disposed but appear to be rather lens-shaped. In all other species they approach a circular outline, are more or less separated from one another, and vary in density from tree to tree. This specifically insignificant variation of density accounts for the description of a variety *subconcolor* under *H. brasiliensis.* This species shows a tendency for many individuals, throughout its entire range, to have relatively fewer, more widely spaced scales which in extreme cases would appear to produce the "subconcolor" condition.

[17] Since this character is frequently hard to distinguish in herbarium material, it is advisable that collectors note it in their observations.

Pubescence: When present, leaflet pubescence is confined to the lower surface. In *H. Benthamiana* and *H. Spruceana* pubescence normally is found over the entire lower surface, associated with the veins and veinlets. In the former species it is usually reddish (occasionally mixed with whitish), while in the latter it is whitish.

In *H. guianensis* and *H. guianensis* var. *lutea* varying amounts of whitish or reddish-tinged pubescence normally are found associated with the midvein. In the latter the tendency is towards reddish or mixed reddish-tinged and whitish pubescence. In *H. guianensis* var. *marginata*, a slight whitish pubescence generally is associated with the midvein but may be harder to distinguish than in the previously mentioned members of the complex[18]. Type specimens of *H. pauciflora*, as well as those of *H. confusa* and *H. pauciflora* var. *coriacea*, all show very slight whitish pubescence associated with some portion of the midvein, usually within the upper half.

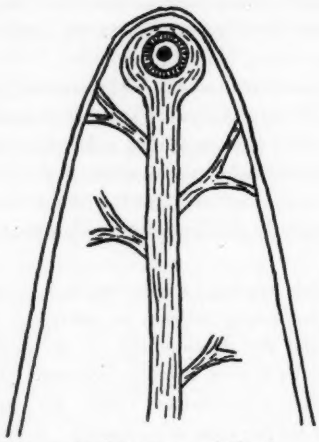
All the other species normally are without pubescence. Frequently, at least in *H. brasiliensis*, the very young leaflets may show some pubescence during the first days of their appearance. These minute hairs, however, soon are entirely caducous. Their presence or absence varies from plant to plant. There are specimens referable to *H. brasiliensis* in which pubescence can be noted along the midvein and even the lateral veins. Close observation, however, has given additional morphological evidence that they probably are introgressive hybrids.

Shape and Size: In many respects these features, especially the size, should be given very little significance. In the past, they have been responsible for perhaps more confusion and promiscuous varietal description than anything else. Size varies with the age of the plant; it varies from year to year depending on climatic conditions; and most noticeably it varies with the portion of the flush from which the leaves are taken. As a general rule, *H. microphylla* has the smallest leaflets within the genus, while *H. brasiliensis* produces some of the largest. It is not uncommon on any one flush of *H. brasiliensis* to find leaflets ranging in length from 5 cm. to 20 cm. or longer.

Shape at least is more constant for the individual than size. In general, *H. microphylla* has a narrow lanceolate leaflet, while *H. guianensis*, particularly var. *marginata*, tends toward an obovate outline. *H. pauciflora, brasiliensis* and *rigidifolia* usually have broadly lanceolate leaflets.

Leaflet Tips: Leaflet tips are a good character to use in distinguishing *H. rigidifolia* and *H. pauciflora*, which from sterile material alone frequently may be hard to tell apart. Rather voluminous material of *H. pauciflora* has failed to reveal a case in which the midvein extends all the way to the end of the blade tip. Furthermore, the end of the midvein always appears to be excised or calloused, and on mature leaflets produces a "socket" or glandular effect (text-fig. 3). This char-

[18] It should be stated that care must be exercised, particularly in the study of herbarium specimens, in distinguishing correctly between pubescence and simulated pubescence caused by hyphae and small fruiting bodies of certain minute fungi which protrude from the midveins. Apparently the veins form an excellent medium of fungus growth during the drying stage of the specimens.



Text-fig. 3. Leaflet tip on which the midvein terminates short of the blade tip and is glandular-calloused. Typified by *H. pauciflora.*

Text-fig. 4. Leaflet tip on which the midvein extends to the end of the blade tip and is not calloused. Typified by *H. rigidifolia.*

acteristic is unique in the genus. It is in strict contrast to *H. rigidifolia* where the midvein extends to the end of the long, narrowly acuminate blade tip, producing a cuspidate effect (text-fig. 4). In other species the midvein also extends to the end of the blade tip or even slightly beyond, as occasionally noted in *H. microphylla* and *H. brasiliensis.*

Texture: Hard coriaceous leaflets are found in *H. rigidifolia.* In *H. pauciflora* the leaflets appear to mature so slowly that a coriaceous condition can be expected only in the fully mature flush of perhaps several months of age. A coriaceous to subcoriaceous texture is the general rule for *H. guianensis* var. *marginata,* and to lesser extents in *H. guianensis, guianensis* var. *lutea, nitida,* and *Benthamiana,* especially when growing under poor soil and climatic conditions.

*H. brasiliensis, microphylla* and *Spruceana* are typified by membranaceous leaflets with considerable individual differences that are distinguishable as good clonal variations.

Margins: Revolute margins are the rule in *H. rigidifolia.* They are noticeable on the mature leaflets of *H. pauciflora* and form the main character in segregating the variety *marginata* from *H. guianensis.*

*Inflorescence.—*

The inflorescence arises from the terminal (occasionally axillary) bud regions of the young stems. It is composed of numerous panicles arising from the axils of the upper scales of the short-shoot. In a majority of the species panicles also arise from the axils of the lower scale leaves of the young flush and frequently from the axils of many of the flush leaves themselves. Under ideal growing condi-

tions trees will commence flowering when between three to five years old. Under forest conditions slow, competitive growth may prevent flowering until the tree is twenty to twenty-five years old.

The flowers of the inflorescence always are monoecious. The terminal flower of the primary and stronger secondary axes of the panicles is pistillate, all others being staminate. Flowering occurs normally once a year, following a dormant or wintering season during which some of the species defoliate completely, *H. brasiliensis* being an example. Other species, however, tend to flower without defoliation. Still others only partially defoliate or gradually defoliate during flowering or after subsequent flush development.

Thus far I have been able to make field studies on only two species with reference to inflorescence habits and their interesting relation to wintering (defoliation or non-defoliation), short-shoots, and the development of the flush. This inter-relationship between the various species is very strongly suggested by meager and incomplete herbarium collections from the Amazon valley, the assumption previously having been that these features are the same in all species. It does appear that a complete comprehension of the genus will be aided materially by a full understanding of the inflorescence and its habits for the different species; a summary of which is suggested under the discussion of leaf persistence.

*Buds and Flowers:* Sketches of both male and female buds and flowers of each important taxonomic entity of the genus are presented in pls. 35, 36, 37, 38, and 39.

The flowers, though small and difficult to dissect, are relatively easy to study after one has mastered the fundamentals of their morphology. With the key here proposed, microscopic dissection of the flower rarely seems necessary, and then only for critical study. Usually sufficient characters may be seen from the superficial bud and flower aspects to make more technical observations unnecessary.

The staminate flower has a short pedicel subtended by a small caducous bract, in the axil of which usually an abortive bud is found. After anthesis the flower abscisses from the peduncle. The perianth is composed of a short calyx tube and five valvate lobes. Petals are absent but a disk is present which may be represented merely as a slight swelling or enlargement of the base of the staminal column, by the presence of five gland-like protuberances, or by five relatively large petal-like acute lobes which seldom reach farther than to the lowest anthers. The anthers range from five to ten in number. They are sessile and attached in one regular or irregular, two irregular, or two regular whorls on a staminal column. The staminal column represents the fused filaments in conjunction with the rudimentary pistil, the tip of which extends beyond the anther whorls and may or may not be slightly lobed or divided giving a stigma-like impression.

The pistillate flower has a somewhat longer pedicel than that of the staminate and likewise abscisses from the peduncle unless it be successfully fertilized. The pedicel dilates into a torus which is conspicuous only in the case of *H. microphylla*.

Here again the perianth is composed of calyx tube and five valvate lobes. Contrary to the habit of the staminate flower, the tube abscisses after anthesis at its point of junction with the torus. Neither petals nor stamens are present but a conspicuous or inconspicuous disk is found. In some cases it is possible to distinguish between petal-like and stamen-like disk lobes. The pistil is present in the form of a tri-locular, tricarpellary ovary, each cell of which has but one ovule. The three stigma lobes may be entire or somewhat lobed and are sessile, though in rare cases they may be very shortly stipitate.

Color: With the exception of *H. Spruceana,* which normally has a dark reddish purple to purplish brown calyx tube, all the species have flowers which are uniformly cream-yellow to brownish yellow in color.

Pubescence: Variation in floral pubescence appears to be of some significance in speciation. In general, the species of *Hevea* have their buds and flowers covered with very short whitish hairs. In *H. Benthamiana* these hairs not only are longer than in other species but have a distinctly reddish color. Within *H. guianensis* and its variety *lutea* there frequently is a reddish tan cast to the short floral pubescence, while the color of the hairs on the peduncles and pedicels tends to be more reddish in tinge. At the point of contact between the peduncle and pedicel there appears to be a narrow band of longer, more dense hairs which is noticeable in *H. Benthamiana, guianensis* and varieties, and *rigidifolia.*

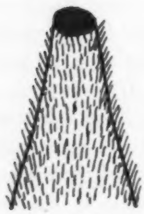
The staminate buds and flowers in all species appear to be rather uniformly pubescent without. The pistillate flowers of four species, however, show remarkable variation. *H. pauciflora,* having pubescent lobes without, is distinctly glabrous below the lobes on the tube and well on the pedicel. *H. microphylla* becomes conspicuously less pubescent on the tube below the lobes and has a glabrous torus and pedicel. The lower-center portion of the lobes of *H. nitida* become glabrous as well as the tube. *H. brasiliensis* is slightly less pubescent on the tube than on the lobes. All other species appear to have uniformly pubescent lobes and tube.

The inner surface of the calyx lobes apparently is somewhat pubescent in all the species, the pubescence being conspicuously longer in *H. pauciflora.*

The ovary, although characteristically short-pubescent or somewhat silky throughout the genus, is definitely glabrous in *H. microphylla* and *H. rigidifolia.* In both *H. pauciflora* and *H. nitida* there is a tendency towards glabrescence.

Calyx Lobe Acumination and Lobe Tips: Bud shape, particularly as to whether it be obtuse or acuminate, has been frequently used as a taxonomic character with special reference to the staminate flower (Huber, 1906). The illustrations (plates 40 and 41) will show the importance of the degree of acumination with reference to the calyx lobes of the mature flower as well as the bud. It should be noted that the degree of bud acumination is not always indicative of the degree of mature calyx lobe acumination; furthermore, that the degree of bud and lobe acumination is not always the same for both the male and female flowers.

5



6

Text-fig. 5. The normal calyx lobe which is acute and pubescent to the tip.

Text-fig. 6. Calyx lobe which is bluntly acute, calloused and glabrous at the tip. Found conspicuously in *H. pauciflora* and *H. nitida*, and less well developed in *H. brasiliensis*.

Two other characters, neither of which appears to have been noted previously, are of importance when taken with the consideration of acumination: (1) Shape of the lobe tips (pl. 43, figs. 1-2), *i. e.*, whether they be acute and pubescent as shown in text-fig. 5, or whether they be blunt and glabrous (calloused) as shown in text-fig. 6. Calloused calyx lobe tips of both staminate and pistillate flowers are found in *H. pauciflora* and *H. nitida*, and to a less pronounced degree in *H. brasiliensis*. (2) The absence or degree of contortion of the bud tip and resulting mature lobes. Contortion in its most pronounced degree is found in both the staminate and pistillate flowers of *H. rigidifolia* (pl. 43, fig. 3) and to a lesser degree in *H. brasiliensis* and *H. microphylla* (pls. 38-39).

Disk: The disk, both in staminate and pistillate flowers, is a rather conspicuous feature of the genus *Hevea*. It is of taxonomic significance when its development in the various species is compared (see pl. 42). The disk of the staminate flowers appears to represent petals. When lobes can be distinguished their position alternates both with that of the calyx lobes and the anthers of the lower whorl. In the pistillate flower a study of the disk lobes, where conspicuously present, indicates the disk to represent both petals and stamens. Frequently the petal-like lobes alternate with structures which appear to be much-reduced stamens, both filaments and anthers being distinguished. Most frequently the disk lobes are attached to the base of the ovary, but cases have been noted in dissections where they are slightly adherent to the calyx at the point of its abscission.

Like other characters, the disk developments are inclined to show a great deal of transition from one extreme to the other from one to the next species. As in the case of acumination, the same degree of development does not always carry through in a parallel fashion between the staminate and pistillate disk of the same species.

Torus: Morphologically all of the species of *Hevea* can be considered to have a torus in the pistillate flower (pls. 41-42). It is only in *H. microphylla* that it is so pronounced (pl. 43, fig. 2) that it may be used immediately in distinguishing that species from all others. Though not a conspicuous character in the genus, it is rather well developed also in *H. pauciflora*.

Anthers: Each stamen consists of a bilocular, longitudinally dehiscent anther, sessile or nearly sessile and attached directly to the staminal column (see upper figures, pl. 42). The column is composed of fused filaments as well as the rudimentary pistil. This accounts for the columnar portion extending above the anther whorl or whorls and explains why this staminal column tip frequently is found to be so variable within the species, *i. e.*, it may be acute, blunt, long, short, entire, bi-lobed or even tri-lobed.

In taxonomic studies of *Hevea* considerable stress has been paid to anther number, on the basis of which two sections, *Euhevea* Muell.-Arg. and *Bisiphonia* (Baill.) Muell.-Arg., were erected by Mueller-Argoviensis (1865). Through a study of more complete material I have arrived at the opinion that exact number of anthers is of little taxonomic significance within the limits of certain tendencies. These tendencies are towards 5 anthers in one whorl as typified by *H. guianensis* and its variety *marginata;* towards 6–8 or 9 anthers in two irregular whorls in which the upper is the more irregular, as found in *H. guianensis* var. *lutea, Benthamiana,* and occasionally in *Spruceana, pauciflora,* and *rigidifolia;* and towards 10 anthers in two regular whorls of which *H. brasiliensis, nitida* and *microphylla* might be considered typical. However, the number of anthers may vary within the species and between flowers on the same tree. As is to be expected, if there be two whorls, the anthers of the upper alternate in position with those of the lower.

An anther character of perhaps considerable significance, and one not previously stressed, is the size. Anthers within the genus appear to fall into two definite size groups, those which approach 1 mm. in length and those of about 0.5 mm. in length, with no definite recognizable gradation. The nearest approach is in *H. guianensis* var. *lutea,* where both sizes frequently are present in the same staminate flower, but with little size gradation one into the other. So far as I am able to determine, the large anthers are associated only with the *H. guianensis* complex. They appear quite uniformly in the predominant number of 5 in one whorl in both *H. guianensis* and its variety *marginata.* In all other species the anther size approaches 0.5 mm. with the exception of *H. guianensis* var. *lutea* where both sizes may sometimes be present (usually only one or two of the large size). However, it must be remembered that this is an extremely variable and transitional variety in which frequently none of the larger anthers are present on the irregular whorls, but if present are on the lower whorl.

*Fruit.—*

The fruits are disposed terminally on the inflorescence branches but the ratio of developed fruits to the total number of female flowers is perhaps only one to ten or twenty. So far as I know, the fruit of all species tends to hang down due to its weight on the peduncle. Because of the comparatively long inflorescence in both *H. brasiliensis* and *H. pauciflora,* and because the terminal pistillate flower tends to be the one which most frequently develops fruit, the peduncles of these two species seem to be longer than those of the other species, and of course droop more. The departure of the peduncle from the branches of *H.*

*pauciflora* is conspicuous in that it is at a right angle, after which rather sudden drooping occurs. In *H. brasiliensis* and other species, the peduncle departs from the branch at considerably less than a right angle and droops in a more gradual arc.

The fruit is quite uniform throughout the genus, normally being a 3-carpellary dehiscent capsule of relatively large size. The carpels are bivalved, composed of a coriaceous pericarp and a woody endocarp which varies in thickness with the species. Each carpel normally contains one seed. In some trees, particularly noted in plantings of *H. brasiliensis*, the capsules are occasionally 4-, or even 5-, carpelled, all carpels containing a normal, viable seed. Perhaps through abnormal or imperfect fertilization, capsules sometimes mature normally in every respect except for the seeds, which may be rudimentary or abortive in one or more of the carpels.

Three distinct variations in the capsule of *Hevea* occur: (1) The most prevalent type is subglobose in outline with more or less emarginate, mucronate tip. In cross-section, it is distinctly 3-lobed. In dehiscence this type is violently explosive, both the seeds and capsule parts being thrown as much as 15–20 meters. All that remains on the tree is the peduncle and placenta. There appears to be considerable variation in the thickness of the woody capsule walls or endocarp between species with this type of fruit. *H. guianensis* and its varieties, *H. brasiliensis, nitida,* and *pauciflora* tend to have a thick, woody endocarp in which the valves retain their original shape with little noticeable contortion. On the other hand, *H. Benthamiana* and *H. rigidifolia* have a relatively thin, woody endocarp, the valves of which show very noticeable contortion at dehiscence, especially *H. rigidiflora.* (2) The fruit of *H. microphylla* is unique in that its shape is pyramidal, tending toward an acute apex, and is noticeably keeled. The carpel walls are thin and leathery, being composed of a coriaceous pericarp and an almost paper-thin, woody endocarp. Dehiscence is not explosive; rather, the valves appear to open slowly, greatly contorting and allowing the seeds merely to fall. The valves appear to be persistent to the receptacle for a considerable time after dehiscence; the torus of this species is very conspicuous at the base of the fruit. (3) The fruit of *H. Spruceana* likewise is unique for the genus in that it is much larger, ellipsoid to subovoid, obtuse at the tip, and round in cross-section. The carpel walls are composed of the coriaceous pericarp and a very thick, woody endocarp. Although dehiscence is somewhat explosive, there is little contortion of the valves, and they are persistent to the receptacle for some time. The seeds are not thrown far.

*Seeds:* Hevea seeds[19] are similar in shape and color patterns to those of the castor bean, *Ricinus,* but they are, with few exceptions, very much larger and they always lack the persistent caruncle in mature condition. Reserve material has a very high percentage of oil. Length of viability is normally only a few weeks. Exposure to full sun and drought will shorten this period, while packing in a cool,

[19] Wild pigs, Peccary, of which two common types are known locally in Peru as *huangana* and *sajino,* are extremely fond of the seeds. Deer, *venado,* appear to relish the young seedlings coming up under the trees. Wild game is particularly abundant during the *Hevea* seed season, augmented by many members of the Cat family which prey on both the wild pigs and deer.

slightly moist medium can extend it to two or three months. Although abundant moisture and deep shade is essential for seed germination, the young seedlings soon perish if not exposed to rather full sunlight. Various types of seed twinning have been reported but this seems to be rare.

Much consideration has been given to the color patterns of the outer seed surface of *H. brasiliensis* (La Rue, 1919) as a means of identifying individual trees within the species. Color patterns are relatively stable for the individual. It would appear that coloration is of little use in speciation, with the possible exception of *H. Benthamiana,* where the background is light in comparison with the more tannish background of other species. The brown mottling, too, appears to be somewhat clearer and more brilliant than in other species.

Over-all seed size is apt not to be constant, except in *H. Spruceana,* which is longer than any other species. In this connection the length/thickness ratio is the important factor, seeds of *H. Spruceana* being at least twice as long as thick while in all other species the length is less than twice the thickness.

Shape of the seed, especially in cross-section, tends to be relatively constant for the species and can give considerable aid in speciation. The following generalizations may be made regarding shape and other seed tendencies as an aid to species determination:

*H. Spruceana.*—Several unique characters are present in the seeds. They are at least twice as long as thick, in contrast to those of all other species whose length is less than twice their thickness. The longitudinal-section through the dorsiventral plane shows a slight curved (approaching reniform) condition, suggesting a similarity in both shape and size to the kernel of a Brazil-nut. In cross-section, the seed is sharply angled in that the compressed flattened ventral and the two lateral angles formed at the junction between dorsal and ventral surface are very prominent. The dorsal surface tends to be uniformly rounded with a rather faint dorsal angle.

*H. microphylla.*—The seed is unique. It is triangular-ovate in outline, with the smaller end the micropylar end.

*H. brasiliensis.*—Seeds normally are ellipsoid in outline, somewhat compressed on the ventral surface. In cross-section, the dorsal surface tends to be uniformly rounded, as does the more flattened ventral surface. If any angulation is present it is seen at the junction of the two surfaces. It appears that the presence of germ-plasm from other species will produce noticeable effects on the angulation or generally rounded condition.

*H. Benthamiana.*—In general, this species has smaller seeds than *H. brasiliensis* but, like in that species, they tend to be quite rounded. In color, they have the noticeably whitish background and brilliant brown spots in contrast to the tannish background of other species. Here again hybridization, or at least presence of germ-plasm from other species, seems to produce pronounced effects on the shape.

*H. guianensis* and its varieties.—The seeds tend to show a distinctive 4-angled cross-section in which the dorsal sides are longer than the ventral sides, producing a kite-shaped effect. Each side of both the dorsal and ventral surfaces shows a shallow concavity running throughout most of the seed length.

*H. pauciflora* and *H. rigidifolia.*—The seeds show a decided hexagonal cross-section in which two sides are on the ventral surface and four sides make up the dorsal surface. Each of the dorsal sides tends to have a shallow concavity running nearly the entire length of the seed. On the ventral surface the two sides form prominent lateral concavities on the upper two-thirds of the seed but this is replaced by a central concavity on the lower third.

*H. nitida.*—Seeds of this species appear to have the upper half of the ventral surface composed of two lateral concavities, replaced by one larger, central concavity on the lower half. On the dorsal surface there are two shallow concavities. In the cross-section of the micropilar end a 4-angled, kite-shaped effect is produced which is not noted in the basal cross-section. Not enough seeds of this species have been seen on which to base an accurate description.

## Pollination

Very little is known regarding the pollination of *Hevea* in nature. Since the pollen grains are rather sticky, wind can be eliminated as a factor. Ramaer (1935), in certain hand-pollination experiments, found that cross-pollinations were considerably more successful than self-pollinations. Workers in *Hevea* consider that cross-pollination is the rule, but cases are known where a tree isolated from other trees by many miles repeatedly set fertile fruit year after year. There are other cases, particularly in isolated mono-clonal plantings, where certain clones will not set fruit unless planted in close proximity to other clones. The fact that *Hevea* has set fruit wherever it is planted and comes into flower might indicate that no highly specialized insect adaptation is necessary for its pollination. The terminal position of the pistillate flowers on the inflorescence and its major branch axes could indicate that cross-pollination by flying insects might be favored.

One never can find a jungle *Hevea* tree in bloom that is not covered with ants, usually of varied species, including leaf-cutters, occasionally carrying the flowers to their nests. Though ants cannot account for cross-pollination, they may be an important factor in selfing. Maas (1919) states that members of the Nitidulidae, Phlacridae, small Curculionidae, fly species and small bees, have been seen on *Hevea* flowers in the Far East. I have observed the common Honeybee to frequent the flowers of *Hevea* growing at the Plant Introduction Station, Coconut Grove, Florida, but little, if, any, reference has been made regarding the possible pollinators in the natural habitats.

Since we find that natural hybridization is taking place among the species in the Amazon valley, it is imperative to know something of the conditions of cross-pollination and what insects might account for it. *H. brasiliensis*, at least, tends to open its flowers during the latter half of the afternoon but pollen is said to be fertile only for perhaps a day, losing its viability rather rapidly in dry sunny weather (Maas, 1919). The pistillate flower apparently is receptive for two to three days. In view of this, both day- and night-flying insects must be taken into consideration. It would appear that conditions for successful cross-pollination, where species are separated by distances of a mile or less, would be best at night. Within the Peruvian range of *Hevea*, species of stingless bees, both *Melipona* and *Trigona*, have been seen in abundance around and on flowers of *Hevea*. *Melipona*, especially, remains on the flowers even after the felling of a branch. Little seems to be known regarding the distances traveled by members of these genera, but Michener (1946) has made such observations in Panama. It would appear that these stingless bees tend to concentrate on a few trees and work within comparatively limited ranges, accounting mostly for selfing. Dr. Herbert F. Schwartz, of the American Museum of Natural History (correspondence Feb. 5, 1947), has suggested that members of the Megalopta bees (Halictidae) might account in part for the night-flying insects visiting *Hevea*. He has identified a specimen of this group taken from a *Hevea* flower as a species of *Augochlora*. Besides the bees, wasps also are frequent visitors of *Hevea* trees in flower, the nests often being encountered.

At the present time, there appears to be more positive evidence that selfing may be the rule under jungle conditions. Here trees, even of the same species, may be separated by a relatively few meters or up to a kilometer or so. Nevertheless, it must be pointed out that we scarcely know anything of the upperstory fauna in tall forest trees even during the day, much less at night.

## Cytological Summary

According to Baldwin (1947), all the species of *Hevea* thus far studied cytologically have a normal 2n chromosome count of 36, confirming the work of Ramaer (1935), Paddock (1943) and Perry (1943). Baldwin found one individual of *H. pauciflora* to have 18, and another of *H. guianensis* var. *marginata* with 54. Perry (1942) states that "all *(Hevea)* species studied are tetraploid." Ramaer (1935) considered 18 chromosomes as the basic 2n number for *Hevea*. Baldwin believes the normal 36 2n chromosome number likely to be tetraploid, and that the individual with a 54 2n number probably is hexaploid.

## Intraspecific Variation

Some excellent research has been carried on at Far Eastern experiment stations concerning morphological variations of trees of *H. brasiliensis*. No part of the plant's anatomy seems to be without its range of intraspecific variation (Frey-Wyssling, 1931, 1933; Frey-Wyssling, Heusser and Ostendorf, 1932; Assoc. Cent. Exp. Sta., 1939). Furthermore, Bobiloff (1931) has brought out that there are physiological differences between clones of the same species with regard to latex color reactions through the addition of calcium chloride. More recent work is dealing with variations in individual susceptibility to diseases, being carried on by Langford (1945).

Casual observations sometimes lead one to feel that there are more differences between two trees of the same species than between two species. This is especially true when the observer is highly familiar with the details of many clones of *H. brasiliensis* but not with the other species.

My own preliminary observations, as well as those of previous workers, indicate that there is a tendency towards opposing extremes in any one morphological variation; but since the extremes are probably based genetically on multiple factor differences, there are always intermediates present. It also has been observed that though one or many characters may be intermediate in nature, there are other characters which more closely approach one or the other extreme of the total expected variation. A list of variable intraspecific characters can be of material aid in tabulating ranges of variation within species. Large-scale scoring of intraspecific variations, in comparing species, would show amounts of parallel variation ranges between species; and may eventually be used, when more material is available, in showing that a number of species grade one into the other.

Speaking from a more practical standpoint, intraspecific variations are of great value in distinguishing *Hevea* clones. The proper identification of young, sterile,

bud-grafted material or clones in the field planting, budwood garden, and experimental plot is of utmost importance since mixtures due to lack of careful supervision and other unavoidable factors frequently occur and, if not detected, can lead to high production losses.

For the relatively few clones in commercial use in the Far East, the written descriptions amply have served their purpose, even without the actual devising of keys for their identification. The cooperative Hevea Plantation Improvement Program, being carried on by the U. S. Department of Agriculture in cooperation with many of the Latin American countries and commercial rubber companies, has resulted in the amassing and distribution of hundreds of *Hevea* clones selected from superior jungle trees. It also has resulted in the selection of thousands of nursery seedlings from various seed progenies collected throughout the Amazon valley, and is resulting in thousands more of hand-pollinated crosses, all of which are undergoing experimental tests. Once these individuals are proved resistant to strains of the South American Leaf Blight, *Dothidella Ulei,* both under natural and artificial innoculation, they must be distributed to various experiment stations and cooperators for field trials. With each move and each distribution, the chances for an error in labelling increases many-fold.

A comprehensive study of individual morphological variations and their consistency for use in the accurate identification of many clones will in itself be a long-time work. It will be one in which frequent revisions and changes will have to be made to keep abreast of the advancing development and introduction of more and more proved clones into commercial use. The work at first will be largely devoted to the use of vegetative characters to be found on the young budded plants. From this, it will advance to include characters of the mature tree, as bark, latex, trunk and branching. Finally, it must include variations in inflorescence, flower, fruit and seed, which, though not so important for the planter, are necessary for the geneticist and plant breeder.

In making up preliminary lists of intraspecific variable characters, I have, of course, drawn heavily from the previous work on clone characters; but in working with and selecting jungle material and subsequently studying it as young buddings in nurseries, many additional variations have come to my attention. Such would be expected since the new material is coming from widely separated localities and from the jungle instead of from the original stock on which the Far Eastern industry is based. Certainly many other contrasting characters are yet to be observed, and one can readily see that all possible combinations of the many character variations would lead to astronomical figures. There is little reason to doubt that keys could be devised to take care of any number of clones desired to be identified.

The most practical means of large-scale clone identification would not necessarily have to be in the form of a key. The punch-card system might better be adopted in which only combinations of strongly contrasting characters be used, disregarding all intermediates.

The following intraspecific characters are listed with their contrasting conditions which have been found to exist within *H. brasiliensis.* Since the greatest practical need for intraspecific variations lies in the differences on young budded clones, the characters found on young, sterile plants are stressed. I have had little opportunity for practical observation of characters of this sort from large progeny numbers of species other than *H. brasiliensis,* or, for that matter, of many of the known interspecific hybrids. Yet from some such observations made on *H. guianensis* var. *lutea* there is reason to believe that parallel conditions exist in other species. With little revision, these lists of intraspecific variations might well apply to the hybrids as well as the species, after the material in question has been given its proper specific rank.

TRUNK (STEM)—
- GROWTH: strong or weak
- FORM: erect or leaning
- BASAL CROSS-SECTION: round or fluted
- BARK
  - GREEN: with or without bloom
  - BROWN-GREEN
    - LENTICELS: conspicuous or inconspicuous
      - COLOR: whitish or as cork
    - FIRST CORK: on flush or on interflush<br>in streaks or in spots
  - BROWN
    - COLOR: grayish, tannish, reddish or brownish
    - LENTICELS: conspicuous or inconspicuous
      - SIZE: large or small
      - COLOR: whitish or as cork
    - CORK: smooth or rough
      - GROWTH CRACK INTERVAL: fine or coarse
- LATEX
  - COLOR: white, cream or yellow
  - CONSISTENCY: watery or thick
- BUDS[20]
  - TERMINAL
    - BUD SCALES: few or many
      - SHAPE: linear or deltoid
  - AXILLARY: depressed or exserted; early-sprouting or late-sprouting
- LEAF SCAR: protruding or not protruding
  - MARGIN: protruding or not protruding
- STIPULES: conspicuous or inconspicuous<br>early caducous or late caducous
  - SHAPE: linear or deltoid
- TYPICAL FLUSH
  - SHAPE: asymmetrical or symmetrical<br>half-globular or globular segment<br>conical or truncate-conical
  - DIMENSIONS: large or small<br>broad or narrow<br>tall or short
  - DENSITY: sparse or dense
  - STORIES: continuous or separated

LEAVES—
- PETIOLES: longer or shorter than blades
  - DIRECTION: downward, horizontal, or upward
  - FORM: straight, arcuate, inverse-arcuate, or sigmoid

[20]Bud characters could be substantially augmented when considering other species in addition to *H. brasiliensis.*

BASE: normal or much swollen
suberized or not suberized
DIMENSIONS: long or short
thick or thin
PETIOLULES
ANGLE BETWEEN EACH: broad (above 90°) or narrow (below 70°)
DIRECTION: downward, horizontal, or upward
FORM: clawed or not clawed
SIZE: long or short
LEAF BLADES
COLOR: yellowish green, light green, or dark green
PUBESCENCE[21]: absent or present on veins
UPPER SURFACE LUSTRE: glossy or dull
LOWER SURFACE LUSTRE: subconcolorous or not subconcolorous
TEXTURE: membranaceous or coriaceous
SHAPE: lanceolate or oblanceolate
ovate or obovate
diamond or rhombic
suborbicular (orbicular leaflets have not yet been noted)
SIZE: large or small
MARGIN: plane, wavy or crisped
revolute or not revolute
MIDVEIN: terminating short of blade tip, extending to end of blade tip, or extending beyond blade tip
LATERAL VEINS: continuous, forked or branched
TIP: OBTUSE: attenuate (acuminate) or short (not acuminate)
ACUTE: acuminate or not acuminate
BASE: acuminate or not acuminate
obtuse or acute
LONG-SECTION PROFILE: flat or convex
CROSS-SECTION PROFILE: flat, V-shaped or boat-shaped
POSITION TO PLANE OF PETIOLE: erect, semi-erect, parallel, declined or horizontal
POSITION TO EACH OTHER: apart, touching or overlapping
MISCELLANEOUS ABNORMALITIES
LEAVES: more than 3 leaflets
less than 3 leaflets
leaflets concrescent

The above intraspecific variations are but a few when considering that these are found in the young plant. An over-all consideration of the mature trees would include not only the above but would be augmented by many more, some of which have been mentioned under the morphological discussions. A few of the more pronounced intraspecific variations of mature trees may be found in the nature of the corky bark surface, its color, and its method of exfoliation. The color of the phloem is highly characteristic, and five color divisions already have been mentioned. The nature of the branching also can be placed in various classes. Besides the study of variations in seed-color pattern, very little has been done regarding intraspecific variations in the inflorescence, flowers, floral pubescence, fruit and seed shapes, all of which show innumerable variable contrasting characters. However, as yet they are not sufficiently well studied to be presented in this paper.

[21] In considerations including other than *H. brasiliensis*, pubescence characters can be greatly augmented and highly significant.

## KEY TO THE PRINCIPAL SPECIES AND VARIETIES OF HEVEA

A. Leafy shoots (flushes) alternating with relatively elongate, caducous-scaly short-shoots[22] (interflush short-shoots[23]).

- 1. Leaflets distinctly erect to slightly horizontal[24]; staminate flowers without disk lobes; seeds with 4-angled (kite-shaped) cross-section.
  - a. Staminate buds broadly obtuse to rounded (may be somewhat acute in var. *marginata*); anthers about 1 mm. long, normally 5 in one whorl.
    - α. Leaflets membranaceous to subcoriaceous, not revolute ............ 1. H. GUIANENSIS[25]
    - β. Leaflets coriaceous, revolute ............ × *H. guianensis* var. *marginata*
  - b. Staminate buds acute to acuminate; anthers about 0.5 mm. long (one or more may approach 1 mm.), normally 5–7 in two irregular whorls ............ 1a. H. GUIANENSIS var. LUTEA
- 2. Leaflets distinctly horizontal to reclinate; staminate flowers with disk lobes; seeds variously shaped.
  - a. Leaflets concolorous, not lepidote on the lower surface; leaf flush tending to defoliate before appearance of inflorescence, at least before appearance of new flush; staminate disk lobes very conspicuous, attaining lower whorl of anthers ............ 2. H. NITIDA
  - b. Leaflets not concolorous, densely whitish-lepidote on the lower surface; leaf flush usually persistently leafy until after inflorescence maturation and appearance of new flush; staminate disk lobes inconspicuous, short.
    - α. Mature leaflets coriaceous, glabrous below; flowers yellowish; diameter of staminate flowers normal for the genus (about 2.5–3 mm.); pistillate disk lobes conspicuous, long-acute; fruit with 3-lobed cross-section; seeds hexagonal in cross-section, length less than twice the thickness.
      - I. Leaflets conspicuously revolute, hard-coriaceous, cuspidate, midvein extending to end of blade tip, not callose-tipped; staminate buds long-acuminate, conspicuously contorted; calyx lobes acute-tipped, pubescent to tip, not calloused.... *H. rigidifolia*
      - II. Leaflets not conspicuously revolute, membranaceous when young, becoming coriaceous with slow maturation, not cuspidate, with midvein terminating before reaching blade tip, having a glandular, calloused tip; staminate buds obtuse, never contorted; calyx lobes blunt-tipped, the tips calloused, glabrous ............ 3. H. PAUCIFLORA
    - β. Mature leaflets membranaceous, usually noticeably whitish-pilose over entire lower surface; flowers reddish to brownish purple, at least the calyx tube; staminate flowers largest in diameter for the genus (about 4.5 mm.); pistillate disk lobes inconspicuous; fruit with round cross-section; seeds ventrally compressed-angular, otherwise, rounded in cross-section, length at least twice the thickness ............ *H. Spruceana*

B. Leafy shoots (flushes) alternating with narrow rings of bud-scale scars[26] (interflush rings)[27].

---

[22] Refer to text-fig. 1 and pl. 32, fig. 2.

[23] Attention is called to cases where hybridization between species of this group and those in which the short-shoot is not conspicuous has produced rather rare individuals, though otherwise characteristic for the most part of one of the short-shooted species which may not have this feature in evidence.

[24] Position of leaflet frequently of little use in the herbarium.

[25] Species printed in capitals are those represented in Peru; those printed in lower case have not been found to occur in Peru.

[26] Refer to text-fig. 2, and pl. 32, fig. 1.

[27] Attention is called to cases where hybridization has occurred with conspicuously short-shooted species, the short-shoot being usually conspicuous in the hybrid. As is particularly evident in *H. Benthamiana* hybrids, the specimen may superficially resemble that species in most characters except a conspicuous short-shoot.

1. Leaflets usually reddish-pilose over entire lower surface; anthers normally less than 10 in two irregular whorls; seeds showing distinct whitish background under brilliant, clear brown spots..............4. H. BENTHAMIANA
2. Leaflets glabrous below; anthers normally 10, in two regular whorls; seeds showing distinctly tan background under usually dull brown spots.
   a. Leaflets relatively small (5–12 cm. long); flowers very long (staminate about 7 mm.; pistillate about 11 mm.) for the genus, the pistillate with an enlarged torus; calyx lobes acutely acuminate, pubescent to tip, not calloused; both staminate and pistillate disk lobes small but conspicuous; ovary glabrous; capsule pyramidal, acute; valves thin, leathery; seeds triangular-ovate in longitudinal section.......... *H. microphylla*
   b. Leaflets relatively large (5–30 cm. or more long); flowers of median length (staminate 5 mm.; pistillate 8 mm.) for the genus, the pistillate without an enlarged torus; calyx lobes bluntly acuminate, with small calloused, glabrous tips; both staminate and pistillate disk lobes very small and inconspicuous; ovary silky-pubescent; capsule subglobose, emarginate; valves thick, woody; seeds oval in longitudinal section..........5. H. BRASILIENSIS

## The Peruvian Species

1. HEVEA GUIANENSIS Aubl. Hist. Pl. Guiana Fr. 2:871. (*pl. 335* as *H. peruviana*, sphalm). 1775.

*Jatropha* (?) *elastica* L. Sp. Pl. Suppl. 422. 1781.
*Caoutchoua elastica* (L.) H. F. Gmel. Syst. 1007. 1791.
*Siphonia Cahuchu* Rich. ex Willd. Sp. Pl. 4:567. 1805.
*Siphonia elastica* (L.) Pers. Syn. Pl. 2:588. 1807.
*Siphonia guianensis* (Aubl.) Juss. Euphorb. Gen. 40 (*pl. 12, fig. 38a* as *Siphonia elastica*, sphalm). 1824.
*Hevea nigra* Ule, in Engl. Bot. Jahrb. 35:667. 1905.
*Hevea caucho* Posada, Estudios Cient. 212. 1909, nom. nud.
*Hevea collina* Huber, in Bol. Mus. Goeldi 5:249. 1909.
*Hevea guianensis* var. *collina* (Huber) Ducke, in Archiv. Jard. Bot. Rio de Janeiro 4:109. 1925.
*Hevea guianensis* var. *cuneata* (Huber) Ducke, l. c. 6:51. 1933, in part.
*Hevea guianensis* ssp. *occidentalis* Ducke, in Archiv. Inst. Biol. Veg. Rio de Janeiro 2:229. 1935.
*Hevea guianensis* var. *occidentalis* Ducke, l. c. 1935.
*Hevea guianensis* ssp. *typica* Ducke, l. c. 227. 1935.

Medium-sized to large tree to 40 m. tall; trunk cylindrical; branches somewhat reddish; short-shoots very conspicuous, of somewhat greater diameter than the long-shoots; bud scales very numerous, linear, about 6 mm. long, early caducous. Leaves partly persistent until after appearance of inflorescence; mature leaflets erect, membranaceous to thinly coriaceous, usually obovate with short acuminate tip, the pubescence of sparse hairs on lower surface along midvein, tannish or somewhat reddish, the scales of the lower surface roundish, the midvein continuous to end of blade tip, not calloused. Flowers yellowish, staminate buds rounded to obtuse, not contorted, the short pubescence whitish-tan to reddish, rather uniformly distributed except at abscission region of pedicel where the hairs are more dense and longer; staminate flowers about 3.5 mm. long and 3 mm. broad, the calyx lobes acute and acute-tipped, not calloused and not acuminate, the disk inconspicu-

ous, represented by a slight flaring of the staminal column base, the anthers normally 5, approximately 1 mm. in length, in one whorl; pistillate buds obtuse to acutish, not contorted, the pubescence short, uniformly whitish tan to reddish; pistillate flowers about 6 mm. long and 3 mm. broad, the calyx lobes acute and acute-tipped, not calloused, scarcely acuminate, the disk inconspicuous, the ovary silky-pubescent. Fruit maturing green in color, subglobose, emarginate-apiculate with 3-lobed cross-section; capsules ligneous, explosive, the valves thick, showing no contortion at dehiscence; seeds quadrangular-kite shaped in cross-section, to about 20 mm. long and 18 mm. thick, latex sulphur to cream-yellow; rubber and yield rather inferior.

VERNACULAR NAMES: *shiringa debil, jebe debil* (Peru).

KNOWN NATURAL DISTRIBUTION: Upland forests of the Guianas, Venezuela, Colombia, Brasil and eastern north-central Peru.

PERU: DEPT. LORETO: Rio Napo, Clotilde, fl.[28] Sept. 1940, *Skutch 4985*.

*Hevea guianensis* in pure strain appears to have been collected rarely in Peru. Ducke has collected it (No. *1433*, Feb. 2, 1942) from near the mouth of the Rio Yavari on the Peru border, and various collections are reported from the Colombian border on the Rio Putumayo. It appears to reach its western limits on the low *tierra altura* hills on the Rio Napo, extending into the vicinity of Iquitos where collections indicate it to exist in forms contaminated with *H. pauciflora*. Other collections, as the type of *H. nigra (Ule 5895)*, from the upper Rio Jurua, Acre Territory, would indicate *H. guianensis* possibly to exist in Peru on the range of hills east of Contamana which center on the Peru-Acre border between 7° and about 8.5° S. However, there is morphological evidence that the type of *H. nigra* is not pure *H. guianensis* but shows some contamination with *H. pauciflora*. The most notable evidence of such contamination appears on the lower leaflet surfaces, where the scales are angular and quite densely crowded. Specimens which match Ducke's *H. guianensis* var. *occidentalis* likewise frequently show this *H. pauciflora* type of lepidote lower leaflet surface. There is a definite tendency for such trees to have considerably weaker rubber than is ordinarily found in true *H. guianensis*. *H. nigra* and what has been known as *H. guianensis* var. *occidentalis* may represent *H. guianensis* with somewhat stabilized admixture of *H. pauciflora* germplasm. A discussion of Peruvian specimens representing hybrids between *H. guianensis* and *H. pauciflora* is given in the succeeding discussion of Putative Hybrids.

1a. HEVEA GUIANENSIS Aubl. var. LUTEA (Spruce ex Benth.) Ducke & Schultes, in Caldasia **3**:249. 1945.

*Siphonia lutea* Spruce, ex Benth. in Hook. Kew Jour. **6**:370. 1854.
*Siphonia brevifolia* Spruce, l. c. **7**:194. 1855, nom. nud.
*Siphonia apiculata* Spruce, ex Baill. in Adansonia **4**:285. 1864.
*Hevea lutea* (Spruce ex Benth.) Muell.-Arg. in Linnaea **34**:204. 1865.
*Hevea peruviana* Lechl., ex Benth. & Hook. Gen. Pl. **3**:290. 1880.

[28]The following abbreviations will refer to the condition of the examined collection, *i. e.*: fl. = in flower, fr. = in fruit, st. = sterile.

*Hevea lutea* var. *cuneata* Huber, in Bol. Mus. Goeldi 3:357. 1902.
*Hevea cuneata* Huber, l. c. 4:626. 1906.
*Hevea brasiliensis* var. *cuneata* (Huber) Pax, in Engl. Pflanzenreich 4:123. 1910.
*Hevea guianensis* var. *cuneata* (Huber) Ducke, in Archiv. Jard. Bot. Rio de Janeiro 6:51. 1933, in part.
*Hevea lutea* var. *pilosula* Ducke, l. c. 6:53. 1933.
*Hevea lutea typica* Ducke, l. c. 1933.
*Hevea lutea* f. *pilosula* Ducke, in Archiv. Inst. Biol. Veg. Rio de Janeiro 2:224, 231. 1935.
*Hevea guianensis* var. *lutea* f. *peruviana* (Lechl. ex Benth. & Hook.) Ducke, in Inst. Agr. do Norte, Bol. Tec. 10:24. 1946.

In general, as *H. guianensis*, but somewhat larger trees with leaflets erect to somewhat horizontal, tending toward broadly lanceolate and having more distinct pubescence along the midvein. Male buds and calyx lobes slightly but distinctly acuminate; anthers normally 5–7, in two irregular whorls, occasionally with one or more anthers of the lower whorl approaching 1 mm. in length, all other anthers about 0.5 mm. Female buds and calyx lobes somewhat acuminate. Seeds very distinctly quadrangular-kite shaped.

From sterile material alone this variety frequently is hard to distinguish from *H. guianensis*. The floral morphology, which in the two extremes is quite distinct, frequently shows intergrading characters.

Vernacular Names: *jebe debil, jebe debil de altura, jebe amapa, shiringa debil, shiringa de altura, shiringa de cerro, shiringa amarillo* (Peru).

Known Natural Distribution: Upland rain forests of Colombia, Brasil, Bolivia and Peru.

Peru: dept. huanuco: Rio Huallaga: Tingo Maria, upland forest, alt. 675–765 m., fl. Dec. 1942, *Baldwin 2824*, fl. Aug. 1940, *Skutch 4963, 4966*, old fr. March 1946, *Seibert 2404, 2406, 2407*. Rio Pachitea: Pto. Inca, fl. and old fr. Oct. 1945, *Seibert 2184*, old fr., *2185*. dept. san martin: Rio Huallaga: Rio Azul, alt. 800 m., fl. and old fr. July 1945, *Seibert 2087;* Rio Pucarte, st. Aug. 1945, *Langamack s. n.*, old fr. Dec. 1945, *Seibert & Langamack 2261, 2262*. dept. loreto: Rio Huallaga: Yurimaguas, upland forest, st. Dec. 1942, *Baldwin 2826, 2827*, fl. Aug.-Sept. 1929, *Killip & Smith 28706;* Rio Paranapura, Chambira Brook, st. May 1943, *Fletcher s. n.;* Rio Shishinagua, st. May 1943, *Fletcher s. n.* Rio Marañon: Pongo de Manseriche, 1923, *La Rue s. n.;* near Borja, fl. Sept. 1940, *Skutch 4980*, st. *4981, 4982*. Rio Ucayali drainage: Rio Yurac Yacu, Boqueron, alt. 1000 m., old fr. July 1945, *Seibert 2078;* Pampa del Sacramento: Cerro de Chanchahuayo, st. Oct. 1898, *Huber 1377* (type of *H. cuneata* Huber); Rio Yurac Yacu, old fr. July 1943, *Seibert 2074;* Rio Aguaitia, fr. Dec. 1944, *Seibert 1978*, st. Nov. 1945, *Seibert 2234*, fr. *2236*. Rio Ucayali, Requena, st. Jan. 1947, *Carpenter & Lescano s. n.* (P-151 grown from seed at Estación Experimental, Tingo Maria). Rio Amazon: Pinto Cocha, Rio Nanay, st. June 1929, *Llewelyn Williams 818;* near mouth of Rio Nanay, st. Dec. 1942, *Baldwin 2822, 2823;* Rio Napo, Singapor, fl. Oct. 1943, *Seibert 1848*, st. *1850;* Rio Ampiyacu, old fr. Feb. 10, 1943, *Russell s. n.;* Huanta, fl. Oct. 1943, *Seibert 1855*, fl. *1856* (intermediate between *H. guianensis* and its variety *lutea*), st. *1857;* Oro Negro, Rio Moto Huayo, old fr. Oct. 1943, *Seibert 1854*. dept. puno: San Gavan, fl. *Collector?* (*H. peruviana* Lechler ex herb.). dept. cuzco: Quince Mil, 1000 m., old fr. May 1946, *Seibert 2426*. dept junin: Satipo, 800 m., old fr. Jan. 1946, *Seibert 2370, 2371;* fl. Sept. 1940 *Skutch 4974*.

Bolivia: Colonia, Rio Negro, fr. July 1943, *Baldwin 2961*.

*Hevea guianensis* var. *lutea* is perhaps the most widely distributed entity of the genus. It is a characteristic tree of the Peruvian *montaña*[29]. It is found on

[29] The term *montaña* in Peru refers to all of the heavily forested land east of the Andes. It includes the eastern Andean foothills, as well as the low expanse of the upper Amazonian basin.

much of the Peruvian *tierra altura* and hilly land of the Peruvian Amazon basin, above the flood levels of the Ucayali, Huallaga, Marañon, Napo and the Amazon. It also is found on the eastern Andean foothills, occasionally as high as 5000 feet. As an entity the variety is extremely variable and frequently appears to grade into *H. guianensis*, with which it certainly is most closely allied.

On the basis of floral morphology and pubescence, both on the flowers and lower leaflet surfaces, *H. guianensis* var. *lutea* frequently shows strong tendencies toward *H. Benthamiana*. Morphological evidence might well suggest its having been derived through the hybridization of *H. guianensis* and *H. Benthamiana*, from which was established a true-breeding, relatively stable, but highly variable entity. An occasional plant, although growing far from the known distribution range of *H. Benthamiana*, appears among typical *H. guianensis* var. *lutea* as a probable recombination or throw-back in certain of its aspects to be more referable to *H. Benthamiana*.

In habit and habitat the variety *lutea* is similar to *H. guianensis*, being a rather large tree and, so far as I know, always found on the *tierra altura*. Though frequently seen close to periodically inundated areas, it appears to be confined to the land above inundation level. The position of the leaflets is erect to semi-erect, like that of *H. guianensis* or at most intermediate between that and the horizontal position characteristic of *H. Benthamiana*. Leaflet size and shape, being variable, show a tendency towards an intermediate condition.

The pubescence on the lower leaflet surface is interesting. It will be recalled that in *H. guianensis* there may be slight, sparse whitish pubescence along the midvein, while in *H. Benthamiana* there is typically a rather dense reddish pubescence over the entire lower surface, associated with the veins and veinlets. The indument of *H. guianensis* var. *lutea* is extremely variable. It ranges from sparse whitish to mixed whitish and reddish, or reddish on the midvein and frequently extending to the secondary or branch veins. One case has been found (*Ray Russell s. n.*, May 14, 1943, Santa Rosa, near Pinglo, Rio Marañon, Loreto) where dense whitish pubescence occurs over the entire surface associated with the veinlets.

It appears that this variable pubescence character has at least twice accounted for the description of separate entities, namely, *H. lutea* var. *pilosula* Ducke and *H. Foxii* Huber. Such variations, where *lutea* and *Benthamiana* grow close together, may result from further hybridization between the two entities. In other instances these variations may be natural tendencies toward recombination. The range of variation and distribution as known from specimens at hand appear to be too intergrading for any decisive subspecific naming at the present time.

The presence of a distinct interflush short-shoot is strongly established and allied to that of *H. guianensis*, though here, too, there may on occasion exist a

condition that strongly suggests *H. Benthamiana* influence. The inflorescence habit and the tendency for some leaves of the previous flush to remain until after the appearance of the inflorescence are characteristic of *H. guianensis,* but with modifying influence seemingly suggestive of the *H. Benthamiana* deciduousness. The shape of the male bud and lobe acumination of the flower in anthesis suggest none other than an intermediate condition between *guianensis* and *Benthamiana.* An intermediate condition also is exceptionally well shown in the anthers and in the whorl irregularities. The disk, on the other hand, is strictly that of *H. guianensis,* being represented only by a slight flaring of the staminal column base in the staminate flower. Fruit, carpel thickness and seed shape are those of *H. guianensis,* while seed coloration on occasion appears to show weak *H. Benthamiana* tendencies. Latex flow, quality, and color are highly variable from tree to tree and from region to region. In general, the variety *lutea* produces the weak rubber and relatively poor yield of *H. guianensis,* though individual trees may have relatively high flow, relatively good quality, or frequently a whitish latex; all of which may or may not be due to the probable *H. Benthamiana* background in its phylogenetic history.

Where *H. guianensis* var. *lutea* is found within close proximity to other species it appears that hybridization readily takes place under proper conditions. In Peru, specimens indicate that this variety hybridizes with *H. brasiliensis, pauciflora* and *Benthamiana.* Furthermore, evidence of hybridization is not necessarily restricted to the region of close proximity with the other species. Evidence of introgression may be found over considerable distances into the *H. guianensis* var. *lutea* distribution and away from the species with which hybridization must have taken place.

Where *H. guianensis* var. *lutea* comes into the proximity of *H. brasiliensis* in Bolivia, Madre de Dios, and in various places along the Ucayali River, infiltration of *H. brasiliensis* germ-plasm into the *lutea* distribution may be noted from morphological characters. In the Madre de Dios this is perhaps most striking. At Maldonado, *H. guianensis* var. *lutea* comes in from the south and west, stopping rather abruptly at the Rio Madre de Dios. To the north there is at present a gap of some 50 kilometers in which practically no *Hevea* is found. Then suddenly one encounters *H. brasiliensis* from the north and east. It is interesting to note that the *H. guianensis* var. *lutea* from the Maldonado area has considerable infiltration of *H. brasiliensis* germ-plasm, morphologically recognizable. Furthermore, the *H. brasiliensis* germ-plasm appears to have infiltrated some 175 kilometers to the south where a specimen collected by Hodge (*No. 6013*) from the upper Inambari is superficially no different from specimens around Maldonado which show this *H. brasiliensis* introgression. Further to the west, however, as at San Gavan and Quince Mil, one is unable to find morphological indication of *H. brasiliensis* germ-plasm in the specimens of *H. guianensis* var. *lutea.*

The presence of this *H. brasiliensis* germ-plasm is also indicated in the quality of rubber from that area south of the Madre de Dios and east of the Inambari. This area was tapped in the past boom and also during World War II. The rubber is considered as a superior quality *lutea* rubber. Though *H. brasiliensis* itself does not ascend the Rio Pachitea or Rio Pichis, a specimen from Pto. Inca showed strong morphological evidence of its presence within *lutea* and may well account for the superior qualities of weak rubber coming from these areas in general.

From the immediate Iquitos area there are sufficient specimens to indicate strongly the presence of an hybrid swarm on the repeatedly cleared land, some of which is in pasture (pl. 44). Other areas consist of second growth at the present time. From specimens at hand, part of this complex hybrid swarm has resulted from interspecific hybridization of *H. guianensis* var. *lutea* and *pauciflora* in which the majority of the collections show natural segregation to simulate most closely *H. pauciflora.* This appears not to be the entire picture since many other specimens morphologically show segregation of an hybrid swarm between *H. brasiliensis* and *pauciflora.* Here there is likewise a tendency for natural segregation to simulate *H. pauciflora* most closely. Occasionally slight morphological tendencies indicate certain specimens to contain germ-plasm of all three species. However, they are not sufficiently clear-cut or shown in sufficient number of collections to be convincingly measured.

Citation of specimens showing hybridization of *H. guianensis* var. *lutea* with other Peruvian species may be found under the section Putative Hybrids.

2. Hevea nitida Mart. ex Muell.-Arg. in Mart. Fl. Bras. **11**$^{2}$:301. 1874.

*Siphonia nitida* Mart. ex Muell.-Arg., l. c., 1874.
*Hevea viridis* Huber, in Bull. Soc. Bot. France **49**:48. 1902; emend. Huber, in Bol. Mus. (Goeldi) **7**:235–236. 1910.

Small to medium-sized tree to 30 m. tall; trunk cylindrical; branches reddish; short-shoots rather conspicuous; bud scales numerous, linear, about 2 mm. long, very early caducous. Leaves partly persistent until after appearance of inflorescence; mature leaflets horizontal to somewhat reclinate, membranaceous but gradually becoming at least subcoriaceous in late maturity, drying reddish, lanceolate to oblanceolate, acuminate, glabrous, concolorous, the scales of the lower surface lacking or so sparse and minute as not to alter its color or lustre, the midvein continuous to the end of the blade tip, not calloused. Flowers whitish-yellow; staminate buds obtuse, becoming somewhat acuminate, not contorted, the short pubescence white, rather uniformly distributed; staminate flowers about 5 mm. long and 3 mm. broad, the calyx lobes slightly acuminate, blunt-tipped, conspicuously calloused, the disk very conspicuous, stellate with 5 acute lobes reaching the lowest anthers, the anthers normally 10, approximating 0.5 mm. in length, in two regular whorls; pistillate buds acute, becoming long-acuminate, not contorted, the pubescence short, white, becoming very sparse towards the lower center of

the lobes and on the tube; pistillate flowers about 9 mm. long and 3.5 mm. broad, the calyx lobes long-acuminate, deeply incised, blunt-tipped, calloused, the disk very conspicuous, of frequently laciniate lobes to 1.5 mm. long, the ovary somewhat glabrescent. Fruit maturing purplish in color, subglobose, emarginate-apiculate, with 3-lobed cross-section; capsules ligneous, explosive, the valves thick, showing little contortion after dehiscence; seeds angular, in cross-section quadrangular kite-shaped toward the micropilar end, becoming hexagonal toward opposite end, to about 21 mm. long and 13 mm. thick. Latex white to buff, not abundant; rubber very inferior.

VERNACULAR NAME: *puca shiringa. shiringa mapa, jebe debil muerto* (Peru).

KNOWN NATURAL DISTRIBUTION: Apparently both on rocky hillsides and periodically inundated land but closely associated with old sandstone or granitic outcrops apparently of Cretaceous, Triassic, and Precambrian origin. Colombia, Brasil and Peru.

PERU: DEPT. LORETO: Rio Huallaga: Rio Yanayacu, between Rio Huallaga and Rio Ucayali, swampy land, st. Dec. 1898, *Huber 1534* (TYPE of *H. viridis* Huber). Rio Amazonas: Rio Nanay, Iquitos area, st. June, 1929, *Llewelyn Williams 889*. Rio Putumayo: Occidente on the Peru-Colombia border, fl. 1910, *Fox 2* (TYPE EMEND. *H. viridis* Huber)—not examined. CULTIVATED MATERIAL: a living plant brought from the Rio Yanayacu (Peru) by J. Huber, growing at the Jardin Botanico do Museo Goeldi, Belem, Brasil, fl. Sept. 1942, *Archer 7582*, st. Sept. 1931, *Krukoff 1628*, st. Feb. 1924, *La Rue s. n.*

The cultivated specimens cited are of considerable interest since we have so little good material of the species collected from Peru. They appear to represent topotypical cultivated material from Huber's type locality of *H. viridis*. The one flowering collection made by Archer is quite referable to *H. nitida* in floral morphology, the short-shoots and, in general, the leaflets. The lower leaflet surfaces of this and other specimens of the cultivated plant, however, tend to show a minute lepidote condition slightly atypical of *H. nitida*. The scales, notwithstanding, are neither of sufficient size nor density to affect the concolorous aspect. There remains some question, since the leaflets do show a slight *H. brasiliensis* aspect, whether or not Huber's *H. viridis* had some admixture of *H. brasiliensis* germ-plasm.

Having seen only one leaflet from the type of *H. nitida*, Ducke (1935) questioned its affinity with *H. viridis*. Schultes (1945) felt that it should belong with *H. brasiliensis* var. *subconcolor*. Through the excellent photograph, made by the Chicago Natural History Museum, of the entire type specimen of Martius' collection deposited in the Herbarium at Munich, it has been possible to identify *H. nitida* as *H. viridis* with some degree of certainty. The presence of interflush short-shoots, as well as the glossy under-surface of the leaflets, leaves little doubt that *H. viridis* should henceforth be refered to *H. nitida*.

The species appears to be associated with inundable areas along streams but closely associated with, as well as being found on, rocky outcrops or hills of the *catinga*[80] type. *H. nitida* var. *toxicodendroides* (Schultes & Vinton) Schultes is

[80] A light forested, rocky hill is known as a *catinga* in Brasil.

apparently confined to areas of ecological extremes found on the tops of hills jutting out of the Amazon valley floor, in Colombia, as described by Schultes (1944). These hills are flat-topped and may be composed of sandstone, quartzite or granite. They are undoubtedly very old geologically, probably of Cretaceous, Triassic, and in some instances Precambrian age.

Collections of *H. nitida* from Peru are extremely few, and the habitats are not at all well known. Since in Colombia and Brasil the species commonly is associated with the old geologic formations one is incited to look for some indication of similar outcrops in the Peruvian collection areas. Reference to the Geological Society of America's map of South America (1946) indicates such outcrops exist between the Huallaga and the Ucayali, southeast of Yurimaguas. It shows much of the area north of Iquitos, through which the Putumayo passes, to be of Precambrian origin. Although no indication of this is given on Iquitos itself, it must be said that the immediate area on which Iquitos is built is considerably higher than the surrounding country. The soil of this area is not typical of Tertiary deposits of the surrounding lower area, being a yellow, much compacted, clayey sand. It is quite possible that the immediate Iquitos area is itself a relic area. If this is true, the presence of *H. nitida* near Iquitos as represented by the Williams specimen can be satisfactorily explained.

From both Peruvian and extra-Peruvian collections at hand, it appears that *H. nitida* has very widely scattered distributions of rather confined and small areas. This may indicate it to be a survival or relic species. Undoubtedly many more localities of *H. nitida* still exist to be discovered. The same may be said for probable outcrops of these ancient formations jutting out above the Tertiary deposits of the Amazon valley. These probable discoveries will undoubtedly picture more fully the chain of relic areas running southwest from the Guianas and more or less skirting the eastern edge of the northern Andes.

In a number of characters, including floral and fruit structure, habitat association with old geological formations, and the very poor-quality rubber, there would appear to be close relationship of *H. nitida* to *H. pauciflora*. *H. nitida*, however, is easily distinguished by its concolorous leaflets, the exceedingly well-developed staminate disk, and the pronounced acumination of the female bud and mature calyx lobes.

The Peruvian specimens referable to *H. nitida* show no distinct morphological evidence of hybridization with other species. However, it should be stated that the presence of some minute scales on certain specimens could indicate the presence of *H. brasiliensis* germ-plasm. A selection of cultivated *H. brasiliensis*, P-143, from seed collected at Cuipari on the Rio Huallaga and growing at Tingo Maria, on the other hand, shows some floral and lepidote conditions that might indicate slight contamination of *H. nitida*. Unfortunately, the number of specimens is insufficient for making accurate measurements upon which to bear out Baldwin's

suggestion (1947) that *H. brasiliensis* var. *subconcolor* possibly resulted from introgression of *H. nitida* genes into *H. brasiliensis*.

3. HEVEA PAUCIFLORA (Spruce ex Benth.) Muell.-Arg. in Linnaea **34**:203. 1865.

*Siphonia pauciflora* Spruce, ex Benth. in Hook. Kew Jour. **6**:370. 1854.
*Hevea membranacea* Muell.-Arg. in Mart. Fl. Bras. **11**²:299. 1874.
*Hevea confusa* Hemsl. in Hook. Ic. Pl. **6**:2, sub *pl. 2570, pl. 2575, figs. 1–3, pl. 2575, figs. 12 & 13.* 1898.
*Hevea membranacea* var. *leiogyne* Ducke, in Archiv. Jard. Bot. Rio de Janeiro **6**:57. 1933.
*Hevea pauciflora* ssp. *typica* Ducke, in Archiv. Inst. Biol. Veg. Rio de Janeiro **2**:239. 1935.
*Hevea pauciflora* ssp. *coriacea* Ducke, l. c. 1935.
*Hevea pauciflora* var. *coriacea* Ducke, l. c. 1935.
*Hevea membranacea* f. *leiogyne* Ducke, l. c. 1935.

Small to large tree to 30 m. tall; branches brownish; trunk cylindrical; short-shoots conspicuous; bud-scales very numerous, deltoid-acuminate, about 3 mm. long, very early caducous. Leaves persistent to partially persistent until after inflorescence maturation and appearance of new flush; mature leaflets horizontal to slightly reclinate, at first membranaceous but slowly becoming quite coriaceous and even revolute in late maturity, usually broadly lanceolate with short obtusely acuminate tip, the pubescence none or of few short, white hairs along part of the midvein, the scales of the lower surface very dense, angular in tile-like compactness, producing a conspicuous whitish surface, the midvein terminating short of the blade tip, calloused or gland-like. Flowers pale yellow; staminate buds obtuse, not contorted, the pubescence white, tomentose, usually dense and rather uniformly distributed; staminate flowers about 3–4 mm. long and 3.5 mm. broad, the calyx lobes acute, blunt-tipped, conspicuously calloused, scarcely acuminate, the disk inconspicuous, but of 5 small gland-like lobes, the anthers normally 10, approximating 0.5 mm. in length, in two regular whorls; pistillate buds obtuse to acutish, not contorted, the pubescence white, conspicuous on the lobes, but scarcely present on the tube and pedicel; pistillate flowers about 5–6 mm. long, 3–4 mm. broad, the calyx lobes acute, blunt-tipped, conspicuously calloused, becoming slightly acuminate, the disk very conspicuous, of acute lobes about 1.5 mm. long, the ovary glabrate to short-pubescent. Fruit maturing purplish red- (or green?) in color, subglobose, emarginate, short-apiculate with 3-lobed cross-section; capsules ligneous, explosive, the valves thick, showing slight contortion at dehiscence; seeds hexagonal in cross-section, quite variable in size, about 13–25 mm. long and 10–18 mm. thick. Latex whitish to tan, oxidizing black; rubber resinous, sticky, very weak and with little elasticity, the yield very poor.

VERNACULAR NAMES: No vernacular names referable to this species have been encountered in Peru.

KNOWN NATURAL DISTRIBUTION: Apparently associated with geologically old (Precambrian, Triassic, and Cretaceous) outcrops on rocky or sandy slopes, frequently

swampy, in light forest, British Guiana, Venezuela, Brasil, Colombia, and Peru.

PERU: DEPT. LORETO: Iquitos, Estrada Morona, marshy second growth, st. Nov. 1942, *Baldwin 2800*, fr. *2801*, *2802*, fl. *2803*, *2805*, *2806*, fr. *2808*, fl. *2809*, fl. and fr. Dec. 1942, *2815*, *2830*. Vic. Iquitos: wet, grassy area, fl. Oct. 1940, *Skutch 4990*, fl. and fr., *4991*, st. *4992*; Mishuyacu, fl. Sept. 1929, *Killip & Smith 29919*; Punchana, fl. Dec. 1942, *Baldwin 2816*, fl. and fr. *2818*; San Juan, fr., Dec. 1942, *Baldwin 2820*.

Although the above specimens are referred here to *H. pauciflora*, it is questionable whether they represent this species in pure strain. As to their composite morphological characters as a whole, they are taxonomically referable to *H. pauciflora*. In general aspect, certain morphological details of the flowers and seeds, habit, habitat, variable flowering and fruiting time, there are perhaps more than faint indications of germ-plasm infiltrations from *H. brasiliensis* and *H. guianensis* var. *lutea*.

The *H. pauciflora* complex appears to be one of the older entities of the genus. It has a wide range of distribution, but is limited within that range to what appears now to be a belt of small isolated habitats extending from Iquitos in a general northeasterly direction to British Guiana. These habitats become progressively more numerous, somewhat merging into a large area of distribution in southeastern Venezuela and British Guiana. This complex also appears to limit itself to areas which represent geologically old outcrops jutting through the more recent Tertiary Amazon valley deposits. In this distributional respect *H. pauciflora* is similar to *H. nitida* with which it appears closely related morphologically.

The complex has gone through various phases of taxonomic splitting, in which the Guiana material is usually considered as *H. confusa*. The Brasilian material from the Rio Negro and Solimoes is referred to *H. pauciflora* with coriaceous-leaved specimens as *H. pauciflora* var. *coriacea*. Although Hemsley described *H. confusa* as distinct from *H. pauciflora*, he later (1901) came to the conclusion that it was synonymous with the latter. More recently the feeling has been that *H. confusa* is synonymous with *H. pauciflora* var. *coriacea*.

In my comparative morphological studies of material from the entire known range of the complex, it has become apparent that the differences in leaflet texture is not inherent, but a condition due to maturity. Unlike most other species (possible exceptions are *H. nitida* and *H. rigidifolia*), the leaflets of *H. pauciflora* appear to take a relatively long time to reach their full texture maturity. Although the leaflets reach mature size very shortly after their appearance, they are at first quite membranaceous and for several months gradually become coriaceous. This species tends to hold its leaves until after the appearance of the new flush and the new leaves have reached mature size. Through actual specimens, it has been possible to see the previous year's coriaceous, revolute leaflets, and at the same time see the current year's mature, membranaceous leaflets. This leads me to believe that no valid varietal difference can be made on the basis of leaflet texture. A search has been made, with little success, to find other morphological characters sufficiently stable to base taxonomic segregation of these supposed entities. The specimens at

hand show some striking variations in fruit and seed size, though perhaps no greater than is the range in *H. brasiliensis*. The seed shape would appear, however, to be of a rather uniform pattern, having an hexagonal cross-section. There are so few specimens of the *pauciflora* complex having seed that I am unable to determine whether or not the seed differences are of varietal or subspecific value.

Spruce (Bentham, 1854) has mentioned that the seeds of *Hevea* on the Rio Negro are prepared and eaten by the Indians; and Dr. Baldwin informs me that *H. pauciflora* is frequently grown by the Indians in their yards for the seeds which they eat (Baldwin, 1947). It could be possible that in the hundreds of years Indians have been along the Rio Negro, they have not only distributed the species outside of its natural habitats, but also subconsciously selected for seed size. Perhaps some of the exceptionally large-seeded specimens are coming from old planted trees.

A further character which may or may not be of taxonomic use in the complex lies in the color of the maturing fruit pod. Apparently it usually matures purplish red, but sometimes the color appears to be green. Until further evidence can be shown that valid morphological differences of taxonomic significance exist within the complex, it seems best to consider the complex as one entity under *H. pauciflora*. It is recognized that there appear to be few genetic boundaries to prevent natural hybridization with other species when natural or man-made conditions are favorable for it. This may be an important factor in the seeming confusion within the *H. pauciflora* complex.

Both *H. humilior* and *H. paludosa* have been described from the immediate vicinity of Iquitos. The type material, in both species, is thought to represent segregating material from an hybrid swarm derived through interspecific hybridization of *H. pauciflora* and *H. guianensis* var. *lutea*. In both *H. paludosa* and *H. humilior* the material most closely simulates *H. pauciflora*, and recent collections have been labeled *H. pauciflora* var. *coriacea* by Ducke. The presence of *H. guianensis* var. *lutea* is morphologically more difficult to distinguish in the types of *H. humilior* than in *H. paludosa;* but, at least through bud acumination and pubescence characters, there can be little doubt of its presence.

If *H. pauciflora* and *H. guianensis* var. *lutea* were the only species concerned in producing the Iquitos hybrid swarm the problem would be relatively simple. The swarm is complicated in that segregates of *H. pauciflora* × *brasiliensis* also appear. Morphological evidence from the leaves, short-shoots, bud acumination and contortion, calyx-lobe acumination, and seed characters can leave little doubt of such a condition existing.

Although specimens show natural segregation most closely towards forms of the *H. pauciflora* parent, there is evidence from cultivated trees planted at Hac. Chanticlair that, given ideal and uniform growing conditions, gradation takes place in the direction of both parents. A discussion of this will be found under

*H. brasiliensis* × *pauciflora* in the section Putative Hybrids. The Iquitos hybrid swarm complex is still insufficiently known and collected to give more than faint, inconclusive evidence that certain specimens show influence of all three species within the same plant. Undoubtedly future collections will show this to occur. Discussion and citation of specimens from the Iquitos hybrid swarms may be found under the section Putative Hybrids.

It seems significant that frequently the same tree is both in fruit and flower at the same time. This is borne out by the range of flowering dates when grouping together all specimens from Iquitos cited as *H. pauciflora, H. guianensis* var. *lutea* × *pauciflora,* and *H. brasiliensis* × *pauciflora.* Flowering appears to occur between July and March; furthermore, it must frequently occur twice a year to account for flowers and mature fruit on the same tree. Segregation along morphological lines not only is taking place, but it appears that the normal flowering time regulator has been upset, or at least modified to fit in with the extremely variable, seasonal conditions from year to year and within the year found around Iquitos. Frequent definite wet and dry periods alternate throughout the year. This could give rise to a set of conditions which, when correlated and emphasized by such man-made conditions as deforestation of the jungle, with resultant grazing and second-growth, could well fit in with the unstable pattern of both frequent and sporadic flowering.

The large-scale man-made changes in the immediate area of Iquitos (pl. 44), and the natural conditions within that area, in which all three parent species exist, together with the few genetic boundaries, would all seem to constitute an ideal set of conditions for the development of such hybrid swarms. Since most of the members of the swarms appear most closely to simulate *H. pauciflora,* it must be assumed that the man-made changes have simulated most closely the habitat of that species.

The immediate area around Iquitos is somewhat higher in elevation than the surrounding country, and the rather compacted, sandy, clay soil is not typical of the surrounding lower areas. It appears that Iquitos might well represent an isolated Triassic or Cretaceous sedimentary outcrop, especially since we do find *H. pauciflora,* a species which in other regions seems to be confined to such old outcrops. Practically all of this Iquitos area has been cut over in the past, not only once but perhaps many times. It was presumably inhabited by Indians long before the coming of white man. Here, then, rises the question suggested immediately following the citation of the specimens under *H. pauciflora:* are these specimens pure strain *H. pauciflora?* It might be possible that *H. pauciflora* in pure strain at Iquitos long since has been destroyed by man, but still persists in the form of an hybrid swarm which is attempting to maintain its identity as *H. pauciflora.*

Even though *H. pauciflora* were not originally indigenous to Iquitos, we know that the seeds of this species were eaten by the Indians of the Rio Negro and that they transported seeds for planting in their yards. It would not be too hard to presume that *H. pauciflora* may have been introduced into Iquitos before white man arrived. Successive introductions of this species along the rivers at various points would have led to a man-induced, natural selection for adaptation to a wide range of habitats.

Food for man is scarce in the Amazonian jungle and the Indian augments his jungle harvests with planted root and seed crops, not only in his garden but frequently at scattered points along his hunting trails. One evidence of this is the presence of several Brasil-nut trees, *Bertholletia excelsa,* near the river between Iquitos and its suburb, Punchana. The Brasil-nut tree apparently is not indigenous as far up the Amazon as Iquitos. Its size, as well as the opinion of the older inhabitants, indicates it to have been planted by Indians long before Iquitos was a modern town. The "peach palm," *pijuayo* or *pifuayo, Guilielma sp.,* a native of the Andean slopes, is found frequently in isolated stands of a few trees on well-drained, ideal camping spots near waterways, apparently all through the Amazon valley. These instances are able further to substantiate a theory that *H. pauciflora,* too, may have been introduced by the Indians.

4. Hevea Benthamiana Muell.-Arg. in Linnaea **34**:204. 1865.

Small to medium-sized tree to 25 m. tall; trunk conspicuously swollen toward base; branches reddish gray; short-shoots inconspicuous, of narrow ring of bud-scale scars; bud scales few, thin, linear-acuminate, about 3 mm. long, very early caducous. Leaves deciduous before the appearance of the inflorescence; mature leaflets horizontal to slightly reclinate, firmly membranaceous, very broadly lanceolate to oblanceolate, shortly acuminate, drying reddish, usually reddish-pubescent below, the scales of the lower surface rather dense, whitish, more or less lens-shaped in outline, the pubescence usually dense, typically reddish over the entire surface, and confined to the veins and veinlets, the midvein continuous to the blade tip, not calloused. Flowers yellowish; staminate buds acuminate, not contorted, uniformly dense, long and reddish-pubescent, the pubescence longer and more dense at the point of abscission; staminate flowers about 3–4 mm. long and 2 mm. broad, the calyx lobes acuminate, not contorted and not callose-tipped, the disk of 5 small but conspicuous lobes, the anthers normally 8–10, about 0.5 mm. long, in two irregular to regular whorls; pistillate buds acuminate, not contorted, densely reddish and longish-pubescent, the pubescence becoming less dense towards the base of the tube; pistillate flowers about 6 mm. long and 2.5 mm. broad, the calyx lobes acuminate, not contorted and not callose-tipped, the disk inconspicuous, of very short lobes, the ovary densely short-pubescent. Fruit maturing green, subglobose, emarginate-apiculate, with 3-lobed cross-section; capsules ligneous, explosively dehiscent, the valves rather thin, not noticeably contorting at dehiscence; seeds ellipsoidal in cross-section, ventrally compressed,

but otherwise rounded with scarcely any indication of angling, about 19 mm. long and 14 mm. thick, the brilliant, clear, brownish mottling having a whitish background. Latex white, abundant, the rubber and yield considered second only to that of *H. brasiliensis.*

VERNACULAR NAMES: Thus far, no vernacular names have been encountered in Peru.

KNOWN NATURAL DISTRIBUTION: Apparently confined to the deeply inundated areas and *igapos*[31] near the major streams along and north of the Amazon, southern Venezuela, Colombia, Brasil, and apparently along the lower Peruvian portion of the Rio Putumayo.

Of this species, I have seen no material of apparent pure strain collected from Peruvian soil. Schultes (1945) states that *H. Benthamiana* occurs along the Rio Putumayo of Colombia below Arica, so it is quite possible it may exist on the Peruvian side as well. I have seen specimens, apparently representing hybridized forms of *H. guianensis* var. *lutea* × *Benthamiana,* from the Peruvian-Colombian Putumayo, which have been referred to *H. Foxii* and *H. glabrescens.* These are discussed under the section Putative Hybrids.

Since no specimens from Peru yet coming to my attention apparently have represented pure strain *H. Benthamiana* I am at present giving no synonymy for the species. However, it has been necessary to revise the descriptive terms for the species in keeping with the morphological revisions of the other Peruvian species. This has been done largely from an isotype specimen of *H. Benthamiana, Spruce 2560,* a very fine specimen collected from the Rio Negro region of Brasil, near Panure on the Rio Vaupes.

Many varieties and forms of *H. Benthamiana* have been described, and it appears that most of them have conspicuous short-shoots, a character which is not conspicuously present in typical *Benthamiana* material. Ducke (1943), Schultes (1945) and Baldwin (1947) recognize that *H. Benthamiana* hybridizes rather readily with the *H. guianensis* complex, *H. pauciflora* and *H. Spruceana.* Examination has shown that many specimens considered as varieties of *H. Benthamiana* simulate it in general, except for having the conspicuous short-shoots. This, as well as the presence of other morphological characters, has convinced me that many of these named varieties are actually the result of very frequent hybridization between *H. Benthamiana* and these other species.

5. HEVEA BRASILIENSIS (HBK.) Muell.-Arg. in Linnaea **34**:204. 1865.

*Siphonia brasiliensis* Willd., ex Juss. Euphorb. Gen. 40, 113, *pl. 12, fig. 38b.* 1824, nom. nud.
*Siphonia brasiliensis* HBK. Nov. Gen. et Sp. **7**:171. 1825.
?*Siphonia Kunthiana* Baill. Etud. Gen. Euphorb. 326. 1858.
*Hevea janeirensis* Muell.-Arg. in Mart. Fl. Bras. **11**$^2$:706. 1874.
*Hevea Sieberi* Warb. Kautschukf. 32–33, *fig.* 1900.
?*Hevea Kunthiana* (Baill.) Huber, in Bol. Mus. Goeldi **3**:349. 1902.
*Hevea brasiliensis* var. *angustifolia* Ule, in Tropenpflanzer, Beiheft **6**:8. 1905.
*Hevea brasiliensis* var. *latifolia* Ule, l. c. 1905.
*Hevea brasiliensis* var. *stylosa* Huber, in Bol. Mus. Goeldi **4**:640. 1906.
*Hevea Randiana* Huber, l. c. 636. 1906.

[31] *Igapo* is a Brasilian word for areas subject to very heavy yearly inundation and which are rather permanently swampy.

*Hevea brasiliensis* var. *Randiana* (Huber) Pax, in Pflanzenreich 4:123. 1910.
*Hevea brasiliensis* var. *janeirensis* (Muell.-Arg.) Pax, l. c. 121. 1910.
*Hevea brasiliensis* var. *acreana* Ule, in Engl. Bot. Jahrb. 50:14. 1914.
*Hevea brasiliensis* f. *typica* Ducke, in Arch. Jard. Bot. Rio de Janeiro 6:55. 1933.
*Hevea brasiliensis* var. *subconcolor* Ducke, l. c. 1933.
*Hevea brasiliensis* f. *subconcolor* Ducke, in Archiv. Inst. Biol. Veg. Rio de Janeiro 2:224. 1935.
*Hevea brasiliensis* f. *Randiana* (Huber) Ducke l. c. 1935.
*Siphonia ridleyana* Cook, in Jour. Wash. Acad. Sci. 31:46. 1941.

Large tree to 50 m. tall; branches grayish brown; trunk cylindrical, but noticeably swollen towards base when growing in periodically inundated land; short-shoots inconspicuous, of narrow ring of bud-scale scars; bud scales few to about 10, linear-deltoid, about 3–4 mm. long, early-caducous. Leaves deciduous before appearance of inflorescence; mature leaflets reclinate, membranaceous, usually lanceolate to broadly lanceolate with rather long-acuminate tip, glabrous, the scales of the lower surface whitish and roundish in outline, the midvein continuous to end of blade tip or extending slightly beyond, not calloused. Flowers creamish yellow; staminate buds noticeably acuminate, slightly contorted, the pubescence short, white, uniformly distributed; staminate flowers about 5 mm. long and 2.5 mm. broad, the calyx lobes acuminate, blunt-tipped, calloused, and contorted, the disk inconspicuous, of 5 rudimentary lobes or swellings, the anthers 10, approximating 0.5 mm. in length, in two regular whorls; pistillate buds noticeably acuminate, slightly contorted, the short pubescence white, becoming sparsely distributed below the lobes on the tube; pistillate flowers about 7 mm. long and 3 mm. broad, the calyx lobes long-acuminate, blunt-tipped, calloused and contorted, the disk inconspicuous, the ovary silky-pubescent. Fruit maturing green in color, subglobose, emarginate-apiculate, with 3-lobed cross-section; capsules ligneous, explosive, the valves thick, showing no contortion at dehiscence; seeds ellipsoidal in outline, ventrally compressed but usually without noticeable angling in the ventrally compressed ellipsoidal cross-section, variable in size, 16–38 mm. long, 14–24 mm. thick. Latex white or rarely cream to yellowish; rubber and yield superior for the genus.

VERNACULAR NAMES: *jebe fino*, *shiringa fino*, *shiringa legitimo*, *shiringa* or *seringa* (Peru), and *seringueira* (near the Peru-Brasil border).

KNOWN NATURAL DISTRIBUTION: Periodically inundated land along the Amazon and the lower courses of its larger tributaries in Venezuela, Colombia, Brasil and Peru. Also on well-drained inter-river plateaus or gently rolling land in Parana, southeastern Amazonas, Acre and northern Matto Grosso, Brasil; Pando, Beni and northern La Paz, Bolivia; and Madre de Dios, Peru.

PERU: DEPT. SAN MARTIN: Rio Huallaga above Yurimaguas, periodically inundated land along Rio Cuipari (seed grown at Estación Experimental Agrícola de Tingo Maria), fl. Aug. 21, 1946, *Carpenter & Lescano s. n.* (P-142), fl. Sept. 1946, *Carpenter & Lescano s. n.* (P-143), fl. Aug. 1945, *Seibert 2273*. DEPT. LORETO: periodically inundated land: Rio Marañon, confluence with Rio Ucayali, st. Dec. 1942, *Baldwin 2828*. Rio Pacaya, affluent of Rio Ucayali, st. Mar. 1943, *Russell s. n.* Rio Tapiche, affluent of Rio Ucayali, Uscar, st. Nov. 1943, *Seibert 1893*; Callao, st. Mar. 3, 1943, *Russell s. n.*, st. Mar. 4, 1943, *Russell s. n.* Rio Ucayali, Lago Curuhuaiti, above Requena, st. Nov. 1943, *Seibert*

*1882, 1883, 1884.* Rio Amazon: Rio Itaya, st. May 1929, *Llewelyn Williams 206;* Iquitos: Punchana, st. Dec. 1942, *Baldwin 2821*, Pró, fl. Aug. 1929, *Llewelyn Williams 2003;* Yana Mono Island, mouth of Rio Napo, st. Oct. 1943, *Seibert 1877;* Oran, below mouth of Rio Napo, st. Oct. 1943, *Seibert 1853;* Firmeza, across from Pebas, old fr. Oct. 1943, *Seibert 1861;* Quebrada Yanayacillo, st. Oct. 1943, *Seibert 1864*, fl. *1876;* Fortaleza, Rio Peruate, fl. Oct. 1943, *Seibert 1872, 1873*, st. *1874;* La Victoria, fl. Aug.-Sept. 1929, *Llewelyn Williams 2931;* Caballo Cocha, st. Aug. 1929, *Llewelyn Williams 2176;* (From Caballo Cocha seed progeny grown at Tingo Maria) fl. Aug. 1945, *Seibert 2275, 2277*, fl. Aug. 1946, *Carpenter & Lescano s. n.* (P-146), fl. Sept. 1946, *s. n.* (P-146), fl. Aug. 1946, *s. n.* (P-147); Islandia, mouth of Rio Yavari, fl. and fr. Oct. 1940, *Skutch 4987;* Rio Ataquari, Peru-Colombia border, st. Oct. 1943, *Seibert 1869.* DEPT. MADRE DE DIOS: Usually on well-drained land between streams, soil yellowish to reddish, sandy, clay loam: Rio Acre drainage: Iñapari, Centro Viejo, st. June 1945, *Seibert 2053.* Rio Tahuamanu drainage: Iberia: fl. July 1944, *Seibert 1939;* Centro Alianza, st. July 1944, *Seibert 1932;* Centro Arrozal, st. May 1945, *Seibert 2021*, st. June 1945, *2023, 2024, 2025, 2026*, old fr. *2027, 2028, 2030, 2031*, st. *2032*, old fr. *2033;* Centro Brussellas, st. July 1944, *Seibert 1935, 1936, 1937, 1938;* Centro Miraflores, st. Apr. 1944, *Seibert 1904*, old fr. *1905*, st. July 1944, *Seibert 1933, 1934*, fl. Aug. 1945, *Seibert 2130*, fl. and old fr. *2141, 2142, 2143, 2144;* Centro Portillo, fl. Oct. 1944, *Seibert 1955*, st. *1956*, fl. *1957, 1958, 1959, 1960, 1961, 1962, 1963*, st. *1964, 1965;* Centro Primavera, st. June 1945, *Seibert 2060*, old fr. *2062, 2065;* Centro Urquilla, st. June 1944, *Seibert 1925;* Centro Villa Nueva, st. June 1944, *Seibert 1926.*

BOLIVIA: DEPT. PANDO: On well-drained land between streams, soil yellowish loam to sand-clay loam: Rio Acre drainage: Cobija, st. Dec. 18, 1923, *La Rue s. n.* (three collections); "one hour east" of Nazaret, fl. Aug. 1945, *Seibert 2115;* Nazaret to Nauruediño, between Acre and Tahuamanu drainage, fl. and old fr. Aug. 1945, *Seibert 2116;* Ultimatum to Peru border, Rio Tahuamanu drainage, fl. and old fr. Aug. 1945, *Seibert 2120.* Rio Tahuamanu drainage: Porvenir, st. Dec. 23, 1923, *La Rue s. n.* Rio Abuna drainage: Rio Pacahuaris, Santo Domingo, old fr. June 1943, *Baldwin 2955, 2957.* DEPT. BENI: well-drained *tierra altura*: Riberalta: fl. Sept. 28, 1923, *Wier s. n.;* Hac. El Prado, fl. Aug. 1945, *Seibert 2102;* junction of Beni and Madre de Dios rivers, fl. Aug. 1886, *Rusby 885*, Ivon, Rio Ivon, st. Feb. 1922, *White 2378.* Rio Guapore drainage: Lago Guachi, fl. Sept. 1943, *Baldwin 2998.*

Within the Department of Loreto, along the Amazon (upper Solimoes) and its larger tributaries, as the lower Huallaga, Marañon and Ucayali, *H. brasiliensis* is almost uniformly associated with the periodically inundated areas. Very exceptionally, it is associated with the slightly higher, non-inundable land adjoining the periodically flooded areas, though the distance and the altitude between the two habitats may be but a few meters.

As to the origin of *H. brasiliensis* as a species, I hesitate at this time to draw any definite conclusions. Morphologically, it appears to be a complex made up of characters both simulating and distinct from other species. Its leaflets are more reclinate than in any other species except possibly *H. rigidifolia*, which, however, are not very well known from this standpoint. The short-shoots of *H. brasiliensis* are less pronounced than in any other species. Typically it lacks any pubescence on the lower mature leaflet surfaces. The staminate and pistillate calyx lobes are interesting in that they show small calloused tips. Calloused lobe tips are found in no other species except *H. pauciflora* and *H. nitida*, where they are quite pronounced. The calyx lobe tips of *H. brasiliensis* show some variation, but, in general, are less conspicuous, suggesting an intermediate condition between callosity and

the normal acute tip. Both the disk and number of anthers (10, in two regular whorls) appear to be quite constant. The fruit, the valves, and, in a way, the seeds perhaps most closely resemble those of *H. pauciflora*. The lower leaflet surface is strikingly similar to that of *H. microphylla*. As a species, *H. brasiliensis* forms the largest trees in the genus. Its most outstanding feature is its superior latex yield and rubber quality.

In contrast to the preferred habitat of *H. brasiliensis* along the Amazon, its habitat in the northeastern portion of the Department of Madre de Dios and the adjoining regions of Brasil (Acre) and Bolivia consists of well-drained, rolling land. The soil here is a friable, reddish to yellowish, sandy, clay loam of excellent quality. Although very little of this area, even along the major streams, is subject to long-period flooding, the species is not at all common where considerable flooding occurs.

Although throughout much of its range *H. brasiliensis* is associated with periodically inundated conditions, such is not the case in its southwesternmost limits of distribution. Usually it is not found on inundable land in Bolivia, Matto Grosso or in the state of Parana. *H. brasiliensis* of the Tapajos and regions between the Tapajos and the Xingu apparently is found on the well-drained plateau areas above the rivers. Due to lack of sufficient collections it is not clear to me where, or if, there is a distinct zone of transition between upland and lowland *H. brasiliensis*. The critical area for such determination will lie within the southern half of the Brasilian State of Amazonas. Men in Peru who have been in the upper Yavari, the Rio Blanco, and the Rio Maquia, all rivers which have their source from the range of hills along the Peruvian border adjoining northwestern Acre Territory, have reported that *Hevea brasiliensis* gradually takes to the higher, well-drained land.

There are several interesting cases, from both the Peruvian and Bolivian border areas, in which specimens referable to *H. brasiliensis* show various gradations of *H. guianensis* var. *lutea* influence in their characters, and vice versa. As will be discussed under Putative Hybrids between these two entities, there is evidence that the *tierra altura H. brasiliensis* is a geographic race resulting from introgression and ecotypic selection and carries a slight contamination of *H. guianensis* var. *lutea* germ-plasm.

In southern Madre de Dios and the adjoining region of Puno of Peru, and in the Departments of La Paz and Beni of Bolivia, both the limits of *H. brasiliensis* entering from the northeast and *H. guianensis* var. *lutea* descending along the Andean foothills are quite sharp and distinct, a comparatively narrow belt existing between the two (seemingly of varying width) in which very little *Hevea* is found. Typified by the area between Maldonado and the Rio Manuripe in Madre de Dios, and between Rurrenabaque and Mapiri in Bolivia, it is along the border areas of *H. guianensis* var. *lutea* that there appears to be further hybridization between the two entities. This has resulted in a zone of intergradation along the

zone of intergrading habitat between the relatively flat, rolling area of *tierra altura* *H. brasiliensis* and the steep foothill slopes of *H. guianensis* var. *lutea.*

Hybridization between the *tierra baja H. brasiliensis* and *H. guianensis* var. *lutea* is indicated in the following specimens: from *tierra altura* areas on the Rio Pachitea; near the junction of the Marañon and Ucayali, at Nauta; on the lower Napo; and at the mouth of the Yavari. The fact that specimens are found which are intermediate or approach one or the other of the species indicates that natural hybridization occurs between the two entities at any place where conditions are such that the two species come close together. There may be a resulting tendency for simultaneous and parallel development of the upland race of *H. brasiliensis* at many places throughout the Amazon valley.

Citation of hybrid specimens and further discussion may be found under the section Putative Hybrids, where reference likewise is made to interspecific hybridization involving *H. pauciflora.*

## Natural Occurrence and Species Range

The accompanying map shows the distribution of the *Hevea* species in Peru and bordering areas of neighboring countries. Collections and collecting stations of *Hevea* in Peru are far too few upon which to base a complete and accurate distribution map. Little is known of large areas between many collecting stations cited with the species descriptions. It has been necessary to fill in a large proportion of the map with questionable data gained from hearsay, transient rubber tappers, reports of rubber coming from various isolated areas, and from impressions gained through having flown over much of the lowland area of Peru east of the Andes.

Ule (1905) has presented a map showing the region of the entire Amazon valley in which species of *Hevea* are found. It presents a rather good picture of the distribution of *H. brasiliensis* and part of *H. discolor* sensu *H. Benthamiana,* but makes no attempt to show distributions of other species. The picture presented for Peru is very sketchy and incomplete. The map given in Schurz *et al.* (1925), also showing the entire Amazon valley, is not much more complete in that it deals only with *H. brasiliensis* and *H. Benthamiana.* The distribution of *H. Benthamiana* on the Peruvian Amazon and Napo appears to be entirely inaccurate. *H. brasiliensis* distribution in Peru is shown to extend into regions known to have *H. guianensis* var. *lutea,* a very abundant species in that country but not shown on the map. Neither map gives the over-all picture of *Hevea* species distribution in Peru.

It appears that the genus reaches its southernmost distribution of about 16° S. in the Department of La Paz, Bolivia, and its westernmost limits around the Pongo de Manseriche in the vicinity of the Rio Marañon in the Department of Amazonas, Peru. In both these extremes the genus is represented by *H. guianensis* var. *lutea,* as it is for the altitudinal extremes of the genus where it occasionally reaches 5000

feet on the Andean foothills.

Specific distributional features have been discussed under each species, but little has been said concerning plant associations found with the Peruvian *Hevea* species. In many cases these features are not sufficiently known for present discussion. In northwestern Madre de Dios, where Peru joins Brasil and Bolivia, it is significant that *H. brasiliensis* is associated with the Brasil-nut tree, *Bertholletia* cf. *excelsa,* which in this region has somewhat smaller fruit and apparently better-flavored kernels than trees from lower on the Amazon. Here both trees prefer and are usually confined to the well-drained *tierra altura*. Up to as many as eight trees per hectare of *H. brasiliensis,* and slightly less of *Bertholletia,* have been found on average areas of more dense distribution. Neither *Hevea* nor *Bertholletia* is uniformly distributed throughout the entire area. Both appear to be in local "pockets" of from about 10 to 100 sq. kilometers, separated by several kilometers in which the distribution of *Hevea* especially may be quite sparse. These localized areas of dense *Hevea* distribution are known in that region as *centros;* these being subdivided into *colocasiones* in which several *shiringeros* or rubber tappers live more or less together, working their individual *estradas*.

As a whole, the area could be classed as a *Hevea-Bertholletia* forest in which these two species are most frequently encountered and form the largest of the forest giants. This area of Madre de Dios and that adjoining in Bolivia are frequently characterized by having a thick undergrowth of semi-climbing spiny bamboo, *paca, Guadua tomentosa* Hack & Lindn.[32] *(Seibert 2068)*. These mats of *Guadua* undergrowth, *pacales*[33], are frequently many square kilometers in extent in which little other tree growth than *H. brasiliensis* and *Bertholletia* may be found. It appears that the *Guadua* is slowly enveloping the forest, replacing the old trees as they die out and preventing any other trees from gaining a foothold. It is perhaps because both *Hevea* and *Bertholletia* form such old trees that they still persist in these *pacales*. Many *estradas* are at least partially located in these bamboo areas, in which trail maintenance is a difficult and time-consuming task because of the rapid growth and viciously spiny nature of the undergrowth. Ule (1914) has mentioned this bamboo association with *H. brasiliensis* considerably further to the northeast in Brasil, referring it to *Guadua Weberbauri* Pilger.

Unlike the *Hevea brasiliensis* of the Madre de Dios, that of the Amazon and lower Ucayali grows in the periodically inundated land adjoining the rivers where *Bertholletia* is non-existent and *Guadua* is seldom found. The distribution of *H. brasiliensis* in Peru and adjoining Brasil and Bolivia is apparently not too dissimilar to that shown by Record & Hess (1943) for *Swietenia macrophylla*, Coaba, the Peruvian mahogany. Although *Swietenia macrophylla* extends into regions where *H. guianensis* var. *lutea* is found, in the Iquitos area it occurs on the periodically inundated areas skirting the river with *H. brasiliensis,*

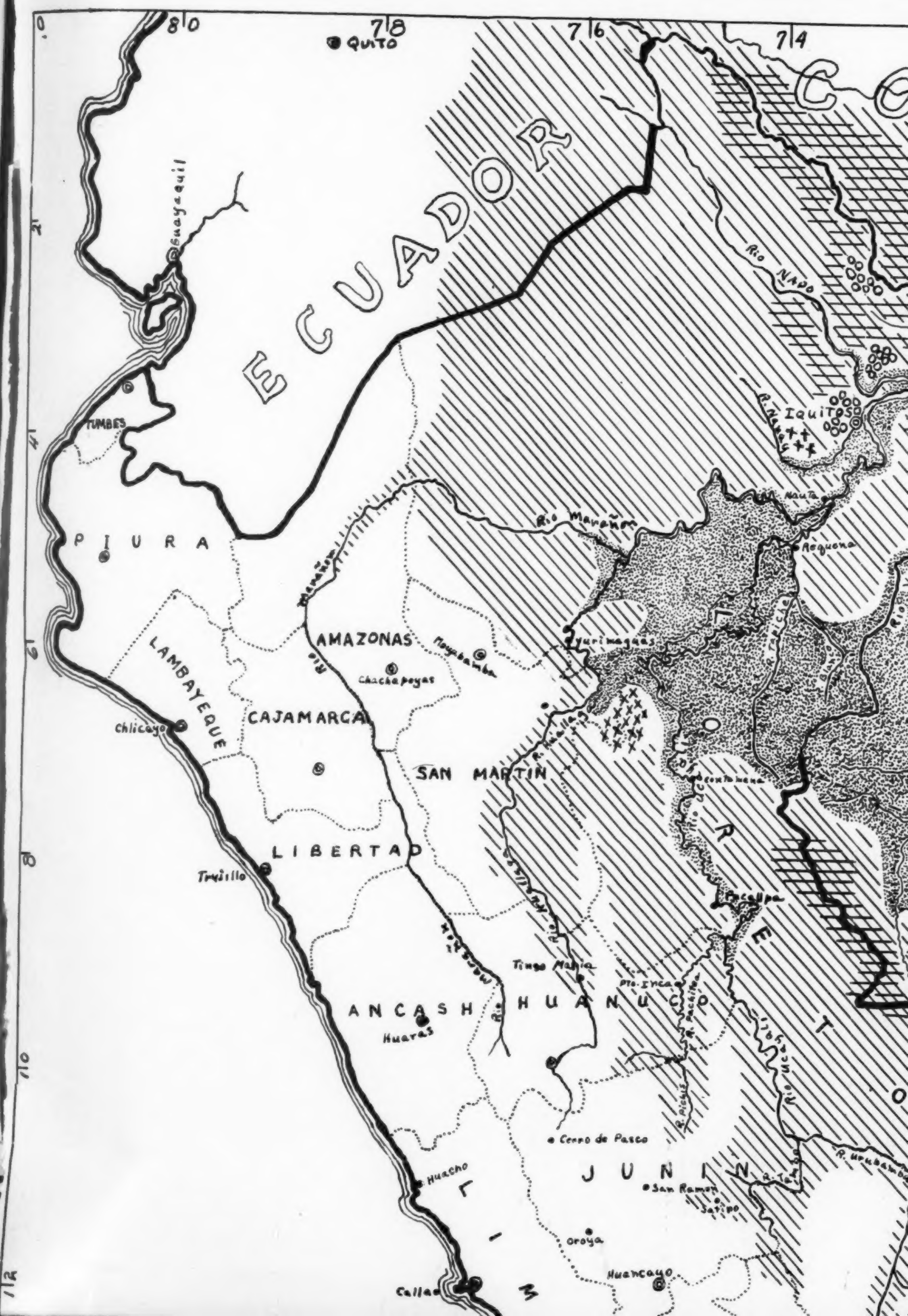
[32] Provisionally determined by Dr. F. A. McClure.

[33] *Pacales* are areas in which the dominant vegetation is *paca, Guadua* sp.

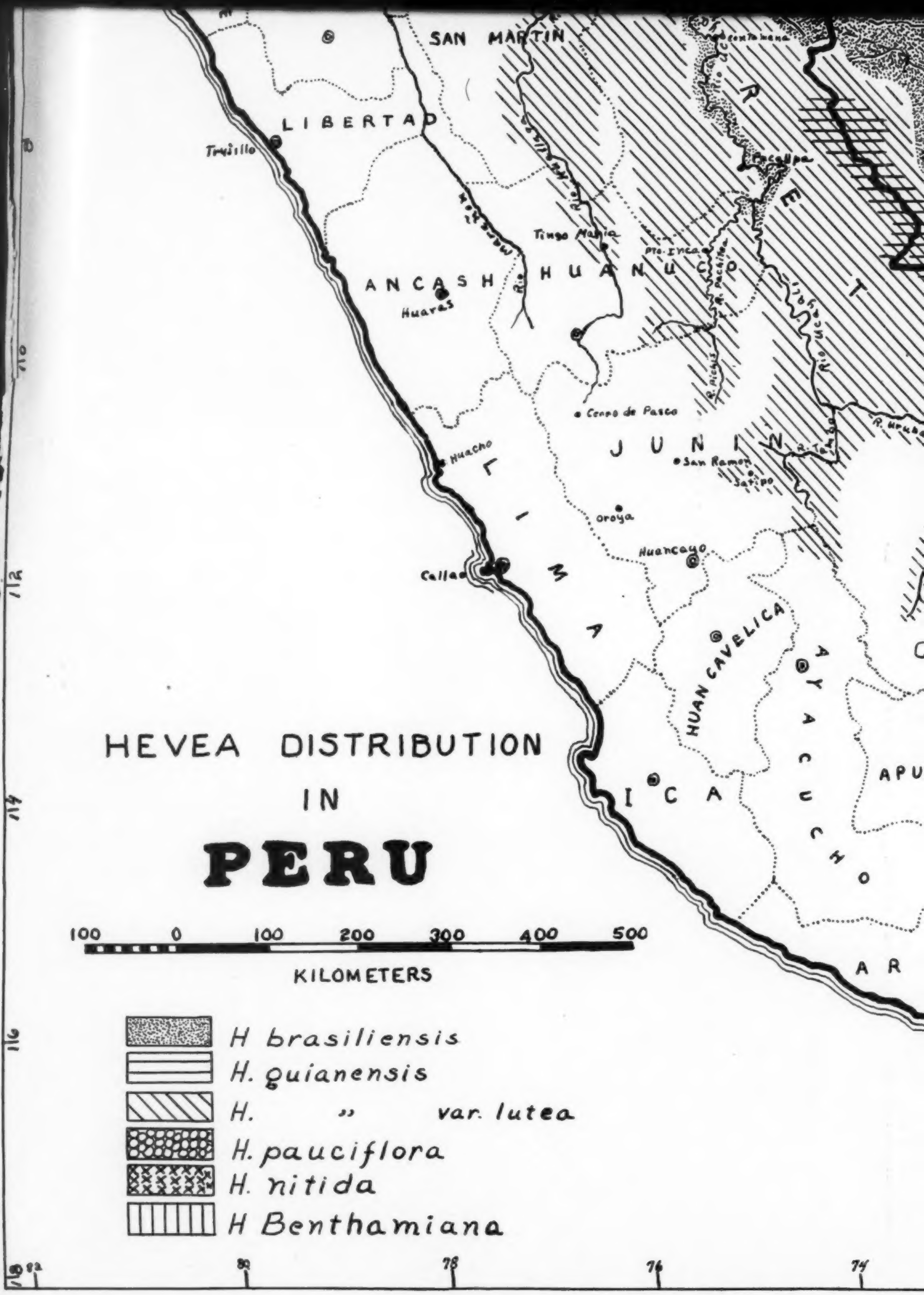
s
r

a
e
e
y
s
-
y
g
-
t
n
g
n.
r-

on
ne
i-
ot
a,
ds
ea
is,

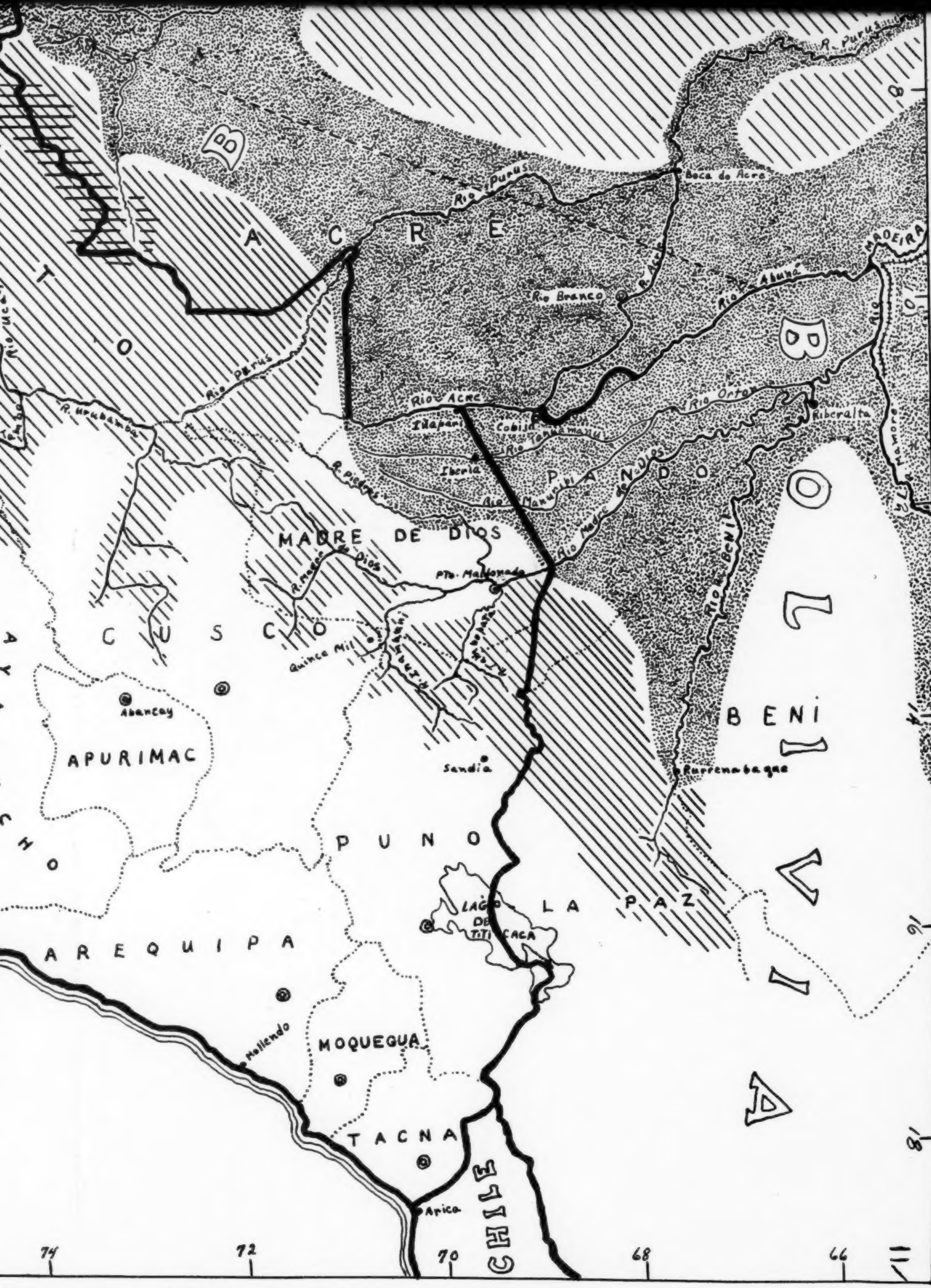

80
78
76
74
QUITO
ECUADOR
Guayaquil
TUMBES
PIURA
LAMBAYEQUE
Chiclayo
CAJAMARCA
AMAZONAS
Chachapoyas
Moyobamba
SAN MARTIN
LIBERTAD
Trujillo
ANCASH
Huaras
HUANUCO
Tingo Maria
Pto. Inca
Cerro de Pasco
JUNIN
San Ramon
Satipo
Oroya
Huancayo
Huacho
Callao
Rio Napo
Iquitos
Nauta
Requena
Rio Marañon
Yurimaguas
Contamana
Pucallpa
R. Urubamba
R. Huallaga
Rio Marañon
Rio Huallaga
R. Pachitea

72
70
68
66
COLOMBIA
Rio Caquetá
R. Apaporis
Rio Japurá
Putumayo
RIO AMAZONAS
R. IÇA
R. Solimões
São Paulo de Olivença
Caballo-cocha
Leticia
Benjamin Constant
Requena
Rio Yavari
R. Jutaí
Rio Juruá
R. Purus
Boca do Acre
Rio Purus
ACRE
Rio Branco
R. Acre
Rio Abuná
MADEIRA
Rio Acre
Cobija
Rio Tahuamanu
Rio Orton
Riberalta
PANDO
Iberia
R. Piedras
Rio Manuripi
MADRE DE DIOS
Pto. Maldonado
Rio Mamoré
R. Urubamba
BENI
2
4
6
8




DISTRIBUTION OF SPECIES OF *HEVEA* IN THE REPUBLIC OF PERU

Base map copied from the Map of the Americas, South America—sheet North, 1:5,000,000, A




BLIC OF PERU AND BORDER REGIONS OF ADJOINING COUNTRIES

h, 1:5,000,000, American Geographical Society of New York, 1942. 5/6 original size.

but appears to make its best growth on the *tierra altura.* In the Madre de Dios area it is found with *H. brasiliensis.*

*Cedrela odorata* in Peru includes in its hillside forest form *cedro virgin,* growing in areas which are typical for *H. guianensis* var. *lutea,* while its *tierra baja* form, found on periodically inundated land in the Iquitos area, is frequently associated with *H. brasiliensis.*

It is not known to what extent the distribution of *H. guianensis* overlaps that of *H. guianensis* var. *lutea* in Peru and adjoining areas. Specimens which are referable to *H. guianensis* appear to exist along with those of *H. guianensis* var. *lutea* in a number of regions. On account of the sparsity of good *H. guianensis* material, no accurate lead can be given as to whether or not the two entities are separated ecologically. It appears that the areas where *H. guianensis* is recognizable taxonomically also contain recognizable hybrids between either *H. guianensis* and *pauciflora* or *H. guianensis* var. *lutea* and *pauciflora.* The distribution of *H. guianensis* as represented on the map is of that which Ducke interprets as *H. guianensis* var. *occidentalis.* This variety has been suggested in the section, Putative Hybrids, as being of introgressive origin. Its distribution might suggest for the most part, that, though in morphological aspect it is referable to *H. guianensis* in that there is a predominance of 5 large anthers in one irregular whorl, it might even have resulted from *H. guianensis* var. *lutea* $\times$ *H. pauciflora.* The conflicting evidence at hand strongly suggests that these areas of overlapping distribution are badly in need of further collection and field study.

This type of distribution mapping, though probably inaccurate in many respects, serves as a much-needed guide in pointing out areas badly in need of further field study and collection. It should be noted that the distribution areas showing *H. nitida* and *H. pauciflora* also are points at which further field study is much needed. Although not plotted on the map, R. de Lemmos Froes recently found *H. Spruceana* to extend up the Amazon to the Rio Jutai, above Fonte Boa. It is very doubtful, however, that this species will ever be found to occur in Peru in pure strain.

## Historical Ecology

In considering the origin and distribution of *Hevea* it will be necessary to have a clear picture of the geological history of the Amazon valley and its surroundings. Though many details are lacking, the Geological Society map for South America (1946) gives the compiled knowledge from existing published works on the subject.

The Andean uplift, which skirts the western reaches of the Amazon valley, peters out to the north and west of the Orinoco River in Venezuela. Previous to the late Mezozoic folding of the Andes, or at least previous to their Pliocene uplift, it is thought that much of the drainage of the present Amazonian region passed towards the Pacific. At that time, it would appear that an older range, still very

prominent in the Guianas (Maguire, 1945) and typified by Cerro Duida (Tate & Hitchcock, 1930) and Mt. Roraima (Tate, 1930) in Venezuela and British Guiana, extended towards the southwest as well as southeastward through the lower, present Amazon region. This range, presumably, was continuous with the ranges still extant which skirt the southeastern reaches of the Amazon valley in Goyaz and Matto Grosso.

The Andean uplift must have stopped the westward flow of water to the Pacific, resulting in a huge, inland lake now evidenced by the Tertiary deposits of the Central Amazonian basin. This lake, in an effort to find an outlet, had to push through the ancient, eastern range. Its rising waters at the same time isolated many higher areas as islands within it. As evidenced by the extremely low divide existing between the Amazon and Orinoco drainage at an actual junction of the upper Casiquiare and the Orinoco in Venezuela, the Amazonian lake may possibly have broken through northward to the Atlantic previous to its present course. Further study of existing maps might indicate that a break once existed at the present low divide between the upper Guapore and Paraguay rivers, flowing out southward through the Parana basin also previous to its final breakthrough and the formation of its present course toward the east.

In light of such complicated geological history as major changes in water-flow to the four directions (referred to as "sloshing" by Baldwin, 1947) and the presence of a huge inland lake in which isolated peaks of an old land mass existed without being flooded, one can begin to picture the genus as having had a complicated genetic history in its adaptation to major ecological changes. Presumably, the genus had its origin on the Triassic land mass or even old Precambrian outcrops at that time and subsequently exposed permanently. If we can base any faith on the presumption that the primitive types of the genus still exist associated with these old formations, we must consider *H. guianensis* and *H. pauciflora* as being those types. From these, and possibly through intergeneric hybridization in some cases with *Cunuria* or other closely allied genera (Baldwin, 1947; Baldwin and Schultes, 1947), other species were derived and ecotypically selected. Such natural selections were for adaptation to a succession of changing water-flow directions, new habitats caused by the draining of the huge lake, and development of the present Amazon drainage system.

Presumably the genus had been evolved previously and was encroaching on the newly formed land as the lake subsided. It is possible that, due to lake conditions and flood waters, seed dispersal at the time could have been in all directions and very widespread through water currents to many portions of the subsiding lake shores. It probably would have been necessary for the genus to evolve types which were adapted to very wet and more or less permanently inundated conditions. Such types are still extant in the form of *H. Spruceana*, *Benthamiana* and *microphylla*, as are types which prefer only periodical inundations as *H. brasiliensis* and *nitida*. Such adaptations have been evolved not only through interspecific

hybridization, chromosome aberrations, and natrual selection, but also possibly through intergeneric hybridization. This may be substantiated by *H. Spruceana* which suggests strong *Cunuria* influence in the structure of its fruit and in habitat preference.

As the lake subsided, leaving the shores high and no longer subject to inundation except along the forming stream channels, there was further need for the evolution of types which could again persist on well-drained land. This habitat was to typify the greater part of the Amazon valley. In the light of this, we find at present that *H. guianensis* var. *lutea* fits into such a habitat pattern and has the largest distribution of any of the species. Also, we find that *H. brasiliensis* has a rather large distribution south and west of the Amazon. It exists not only as a species in areas of comparatively light periodic inundation but in much larger areas of an intermediate zòne on the rather low but well-drained lands below the relatively higher zonal distribution of *H. guianensis* var. *lutea.* As has been pointed out in this paper, there is some morphological evidence that *H. brasiliensis,* as it exists on the *tierra altura,* is ecotypically and genetically different from that which grows on periodically inundated areas, probably having been evolved through introgression of *H. guianensis* var. *lutea* germ-plasm into *H. brasiliensis.*

## Putative Hybrids in Peru

The occurrence in nature of interspecific hybridization in the genus *Hevea,* as evidenced from both wild and cultivated trees, is a fact which can neither be ignored nor questioned. Though intraspecific hybridization within *H. brasiliensis* has long been practiced as a means of *Hevea* improvement in the Far Eastern plantations (s'Jacob, 1931), it is not known accurately when the first artificial interspecific hybrids were produced.

One of the older recognized artificial hybrids is represented in the Herbarium of the Arnold Arboretum by a fine flowering specimen. It was collected at the Singapore Botanic Garden, December 17, 1923, by *Burkill s. n.,* is labeled *H. brasiliensis* × *confusa,* and includes notes concerning the two parents. A study of morphological characters shown by this specimen leaves little doubt but that this hybrid arose from a cross between *H. brasiliensis* and *pauciflora (confusa).* It is of significance that this specimen matches remarkably well two specimens *(Seibert 1840* and *Kuhlman 1727),* collected at Iquitos, Peru, which are of undoubted natural hybrid origin between the same species.

Ramaer (1935) has proved that artificial interspecific hybridization is possible between *H. brasiliensis* and *Spruceana,* and Schmöle (1938, 1941) has reported hybrids from this cross to be superior root stocks for budded clones of *H. brasiliensis* as tested at the A.V.R.O.S. General Experiment Station in Sumatra.

Pearson (1912) and Huber (1913) recognized that hybrid swarms existed between *H. brasiliensis* and *confusa* in the Botanic Garden and plantations in Trini-

dad. Huber then became quite conscious of certain floral and seed variations in trees around the low lands of the Amazon mouth region which appeared to him intermediate between *H. brasiliensis* and *H. Spruceana*. He recognized without doubt that hybridization was occurring between these two species and through comprehensive seed measurements suggested a method of selecting *H. brasiliensis* from *H. Spruceana* and resulting hybrids on the basis of seed size.

As Huber's successor, Ducke (1935, 1943) has devoted sections in his taxonomic works to the recognition and interpretation of natural hybrids occurring in the Amazon valley of Brasil. Furthermore, he has recognized that a number of named species and varieties are of hybrid origin. With additional opinions and evidence presented by La Rue (1926), Cook (1941), Schultes (1945), Baldwin (1946, 1947), and others, it has become necessary to include sections dealing with recognized hybrids in taxonomic works on *Hevea*.

Recognizable natural hybrids are morphologically distinguishable between many of the species and appear in general collections of *Hevea* from many parts of the Amazon valley. It appears that there are no strong genetic barriers between the species. If two or more species come together in their natural distribution and if natural conditions such as flowering time be favorable, natural hybridization may be expected to take place. If ecological conditions be naturally favorable or made favorable by man through clearing, planting, or pasturing, in such a way as to eliminate part or much of the strong natural selection found under normal jungle conditions, the hybridized seed may be expected to, and does, attain the status of mature, flowering and fruiting trees. In the jungle perhaps all but one out of a million seeds meet the fate of being eaten by animals; or, if seeds germinate, the seedlings are eaten by other animals; or the seedlings die within one to four months after germination due to lack of sufficient light on the forest floor. It is an extremely rare seedling which, due to a fallen jungle tree or being along a trail or clearing, ever attains maturity.

HEVEA BRASILIENSIS × GUIANENSIS var. LUTEA

VERNACULAR NAMES: *jebe debil-fino, shiringa debil-fino, jebe debil-fino de altura, shiringa itauba* (Peru).

KNOWN NATURAL DISTRIBUTION: Uusually on or near borders where the two species come together.

The specimens at hand rarely appear to be truly intermediate. In all cases it has been possible to note them as simulating more closely one or the other of the species. The following specimens appear most closely to simulate *H. guianensis* var. *lutea*:

PERU: DEPT. LORETO: Rio Napo, Progreso, st. Oct. 1943, *Seibert 1849*. DEPT. PUNO: Upper Rio Inambari, valley of the Rio Huari-Huari, alt. 1000 m., st. May 1943, *Hodge 6013*. DEPT. MADRE DE DIOS: Vic. Maldonado, south of Rio Tambopata (Seed progeny grown at Estación Experimental Agrícola de Tingo Maria), st. Jan. 1947, *Carpenter & Lescano s. n.* (P-127), fl. Sept. 1946, *s. n.* (P-128), st. Jan. 1947, *s. n.* (P-129). st. Jan. 1947, *s. n.* (P-130).

These specimens, through the presence of erect leaflets and pronounced short-shoots, are referable to *H. guianensis* var. *lutea.* Since most specimens represent selections from seed progeny obtained south of Maldonado, it is unfortunate that only one of these specimens is in flower, that of P-128.. Here the flowers appear intermediate but lack the small calloused tips of *H. brasiliensis.* They have 6–8 anthers in two irregular whorls. The leaflets appear to be intermediate, but have the vein pubescence of *lutea.* As far as is known, the Hodge specimen was taken from a distance of about 175 kilometers from the nearest *H. brasiliensis.* If this be true, here is some interesting evidence of the distance to which introgression can penetrate into species distributions.

*Hevea guianensis* var. *lutea* is characteristic of the eastern slopes of the Peruvian Andean foothills where it occasionally reaches an altitude of 5000 feet. In the southern half of Peru it extends eastward into Bolivia south of the Rio Madre de Dios. Studies made from material originating near Maldonado show it to be superficially characteristic of *H. guianensis* var. *lutea,* but incorporating morphological features of *H. brasiliensis.*

Along the trail from Maldonado north to Iberia, a distance of 211 kilometers, there is a gap of some 50 kilometers between Maldonado and the Rio Manuripe in which *Hevea* scarcely exists. At the Rio Manuripe and to the north, *H. brasiliensis* occurs. From reports, this gap narrows at the Bolivian border east of Maldonado. There is little doubt but that the Maldonado *H. guianensis* var. *lutea* contains established germ-plasm of *H. brasiliensis.* It appears to have been derived through hybridization of the foothill *H. guianensis* var. *lutea* with the approaching *H. brasiliensis* characteristic of the adjoining northeastern Madre de Dios and northeastern Bolivia. In yield and rubber quality the Maldonado material is characteristically intermediate. The short-shoot character frequently is more or less intermediate; and the leaflets are often more horizontal than erect.

The following putative hybrid specimens appear most closely to simulate *H. brasiliensis:*

PERU: DEPT. HUANUCO: Rio Pachitea, Pto. Inca, old fr. Oct. 1945, *Seibert 2186.* DEPT. LORETO: Nauta, st. Nov. 1943, *Seibert & Russell 1881;* Iquitos, Estrada Morona, fl. Dec. 1942, *Baldwin 2829;* Rio Napo, Progreso, st. Oct. 1943, *Seibert 1847;* Rio Yavari, Islandia, st. Oct. 1940, *Skutch 4988.* DEPT. MADRE DE DIOS: vic. Maldonado, south of Rio Tambopata (from seed progeny grown at Estación Experimental Agrícola, Tingo Maria), st. Jan. 1947, *Carpenter & Lescano s. n.* (P-131).

BOLIVIA: DEPT. PANDO: Rio Tahuamanu, Porvenir, st. Dec. 23, 1923, *La Rue s. n.* DEPT. LA PAZ: Isapuri, st. Oct. 1901, *R. S. Williams 1658, 1659;* Mapiri, fl. Sept. 1939, *Krukoff 10824,* st. Sept. 1907, *Buchtien 1622;* Palmos, st. June 1902, *R. S. Williams 1657.*

These specimens appear to show the reclinate leaflets and inconspicuous short-shoots of *H. brasiliensis,* but the leaflets have the vein pubescence of *lutea.* Where flowers are present, the anthers are less than 10 in two irregular whorls. The flowers have intermediate acumination and the calyx lobes occasionally are without small calloused tips. All specimens appear to have been collected from areas above

periodic river inundation. Where it is known, the latex, though yellowish in color, is superior to that normally found in *lutea*.

The La Rue specimen from Porvenir, Bolivia, comes from a region in which *H. guianensis* var. *lutea* is not known. The nearest known occurrence of *lutea* is some 225 kilometers to the south and southwest. Here is a specimen from a center of supposedly pure *H. brasiliensis*, yet it shows *H. guianensis* var. *lutea* characters with little question, even to the inferior rubber and yellow latex. Though this specimen more clearly shows *H. guianensis* var. *lutea* influence than any other I have seen from the Pando-Madre de Dios area, it should be pointed out that *H. brasiliensis* trees with yellow latex and even inferior rubber are not too infrequent. Furthermore, some trees occasionally show slight intergrading characters in the flowers and leaves, discussed under *H. brasiliensis*. The indication is that the so-called Acre-Beni *H. brasiliensis* carries some slight *H. guianensis* var. *lutea* germ-plasm.

It is known that the seed which Sir Henry Wickham took from Brasil to inaugurate the development of the plantation rubber industry of the Far East came from the Tapajos River area near Boim, where the trees grow naturally on well-drained plateau land above any periodic inundation. Early impressions that *H. brasiliensis* grew on inundated land led to test plantings in the Far East on flooded land. It has long since been proved that the plantations did much better on land not subject to flooding, though the trees could live and grow if flooding were not over too long a period of time.

Is there any difference between *H. brasiliensis* from the *tierra baja* and that from *tierra altura?* There seems to be no difference sufficiently distinct to base taxonomic delimitation. Yet, there must be a genetic difference!

Repeated observations of trees and specimens from trees over the entire range of *H. brasiliensis*, and from the two types of habitat, have given some rather good morphological evidence that the *tierra altura*-loving *H. brasiliensis* has been derived through its incorporation of *H. guianensis* (or probably var. *lutea*) germ-plasm. It has been only through the detailed study of a relatively large number of specimens from the Tapajos, Matto Grosso, Acre, Bolivia, and Madre de Dios that certain otherwise unaccountable features sometimes crop up. An occasional specimen will show a tendency toward having a short-shoot. Rather frequently the midveins of the lower leaflet surface will show some pubescence. There may be a strong tendency here and there for the leaflets to approach a horizontal or semi-erect position. Position of the leaflets, one to another, is an interesting feature—varying from apart to touching and to overlapping. The overlapping condition is a rather constant feature of the *H. guianensis* complex. Much has been made of this variable character in clone identification work (Frey-Wyssling *et. al.*, 1932). Frequently, at least in seeds from the Madre de Dios, there is rather strong angularity, approaching the kite-shaped cross-section. Furthermore, there are occasional trees producing cream-colored and, more rarely, sulphur-yellow

latex. Again reference is made to a striking specimen (*La Rue s. n.*, Dec. 23, 1923, "*itauba*", from Porvenir, Bolivia), which combines several pronounced features of *H. guianensis* var. *lutea*. These features are rather conspicuous short-shoots, erect leaflets, and vein pubescence, all in the same specimen. Another specimen (*Seibert 2120*, Ultimatum, Peru-Bolivia border, near Iberia), has the male buds with only slight acumination plus pubescent leaflet veins. These two cases occur in the center of large areas in which only *H. brasiliensis* is represented. There is, it seems, no chance for direct hybridization to have taken place.

It would seem that the establishment of this "ecotype", which resulted from past hybridization, became relatively stabilized superficially as *H. brasiliensis* except for its habitat preference. However, it is still not sufficiently well established to prevent certain morphological throw-backs or recombinations resembling its minor constituent. It may well be referred to as a geographic race derived through ecotypic selection.

If in this discussion the true situation is approached, one can conclude that the plantation industry of the Far East is based not on pure strain *H. brasiliensis* but upon *H. brasiliensis* into which has been incorporated a slight amount of at least *H. guianensis* var. *lutea* germ-plasm.

HEVEA BRASILIENSIS × PAUCIFLORA

VERNACULAR NAMES: None typical of this group has been encountered in Peru.

KNOWN NATURAL DISTRIBUTION: Thus far it has been collected from the vicinity of Iquitos and Caballo Cocha.

PERU: DEPT. LORETO: Iquitos: Marshy second growth on outskirts of city, fl. and fr. Dec. 1942, *Baldwin 2807*, fl., fr. *2810, 2811*; between Iquitos and Morona Cocha in old clearing along swampy stream, fl. Sept. 1944, *Seibert 1940*, fl. Oct. 1940, *Skutch 4993*; Punchana, marshy land, fl. Dec. 1942, *Baldwin 2817*; Mishuyacu, fl. Jan. 1930, *Klug 812*. Caballo Cocha: fl. Aug. 1929, *Llewelyn Williams 2503*.

The above Iquitos specimens are from an hybrid swarm, being most closely referable to *H. pauciflora* through the presence of the conspicuous calloused calyx lobe tips, dense, angular scales of the lower leaflet surface, peduncle departure, and seed characters. The varying degrees of bud and calyx lobe acumination, somewhat reclinate leaflets, and the continuous midvein to the end of the blade tips all show *H. brasiliensis* influence.

In these wild specimens there is not very good evidence of intergrading segregation from one species to the other, since they tend most closely to simulate *H. pauciflora*. The following cultivated specimens taken from a progeny growing at Hacienda Chanticlair on the edge of Iquitos give some experimental evidence that, where natural selection has to some extent been eliminated, there tends to be segregation of intergrading types from one to the other species.

DEPT. LORETO: Hacienda Chanticlair, cultivated in garden, trees 12–20 m. tall, fl. and fr. Sept. 1943, *Seibert 1840*, fl. *1841, 1842, 1843*, fl. *1844*, fl. Mar. 1924, *Kuhlman 1527*.

On the outskirts of the city of Iquitos some 30 trees were planted about

twenty-five years ago from local seed in the garden of Hacienda Chanticlair. The trees show a beautiful series of segregational intermediates between *H. brasiliensis* and *H. pauciflora,* indicating them to be of hybrid origin. At the time of collection some of the trees were partially defoliating, others were in full flower, some with both flowers and maturing fruit, some with mature fruit, while still others were in sterile condition. In size they ranged from 10 to 20 m. tall. The trees had been tapped for a short time at the beginning of the war but tapping was abandoned because of the uniformly low yield of poor quality rubber, high in resin and turning blackish as is characteristic of *H. pauciflora.* The following table will attempt to demonstrate the morphological variations between the two species involved. It is unfortunate that more trees were not in flower at the time of collection to show the complete range of variation which was demonstrated by the group of trees as a whole.

HYBRID SWARM *H. BRASILIENSIS* × *PAUCIFLORA*, HACIENDA CHANTICLAIR, IQUITOS

| | Pistillate disk lobes | Pistillate calyx lobe contortion | Pistillate bud contortion | Staminate disk | Staminate calyx lobe contortion | Staminate bud contortion | Staminate bud acumination | Midvein tip | Scales | Leaf persistence | Short-shoots |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *H. brasiliensis* | 0* | 5 | 5 | 0 | 5 | 5 | 5 | Continuous, not calloused | Round | 0 | 0 |
| Seibert 1840 | 5 | 2 | 1 | 2 | 2 | 0 | 2 | Continuous, calloused | Intermediate | 3 | 4 |
| Seibert 1841 | 2 | 5 | 5 | 1 | 5 | 3 | 5 | Continuous, not calloused | Round | 0 | 5 |
| Seibert 1842 | 0 | ? | ? | ? | ? | ? | ? | Continuous, calloused | Round | 0 | 0 |
| Seibert 1843 | 3 | 3 | 2 | 2 | 0 | 0 | 2 | Continuous, not calloused | Round | 0 | 0 |
| Seibert 1844 | 1 | 5 | 5 | 2 | 2 | 3 | 4 | Continuous, calloused | Round | 0 | 0 |
| Kuhlman 1727 | ? | ? | ? | 3 | 4 | 2 | 5 | Continuous, calloused | Angular | 3 | 4 |
| *H. pauciflora* | 5 | 0 | 0 | 5 | 0 | 0 | 0 | Short of tip, calloused | Angular | 5 | 5 |

* The numbers represent relative degrees to which the character is pronounced.

The group of trees is not only characterized by having very poor rubber, but is relatively free of South American Leaf Blight, *Dothidella Ulei,* a character which appears to be, in the Iquitos region, more inherent in *H. pauciflora* as a whole than in *H. brasiliensis.* This meager evidence would indicate some link between poor quality and low latex yield.

### Hevea guianensis × pauciflora

Vernacular Names: *shiringa bananera, jebe debil muerto* (Peru).

KNOWN NATURAL DISTRIBUTION: Southwestern Colombia, western Brasil, eastern north-central Peru.

PERU: DEPT. LORETO: Iquitos: Estrada Morona, outskirts of city, fl. and fr. Dec. 1942, *Baldwin 2829-A;* Punchana, hillside in old second growth near stream, st. Feb. 1944, *Seibert 2269.* Rio Napo: Curaray, st. Oct. 1940, *Skutch 4986;* 40 kilometers above mouth of Rio Napo, low hills away from river, fl. and old fr. Oct. 1943, *Seibert 1851.*

Although morphologically referable to *H. guianensis* in nearly all respects, the lepidote condition of the lower leaflet surface approaches that found in *H. pauciflora.* The rubber from these trees is extremely poor. It does not retain its shape in ball form after smoking, but rather flattens out, even overnight. The yellowish tan, resiny latex soon oxidizes black to appear as stains on clothing characteristic of banana juice stains—thus the vernacular name, *bananera.* Too little material from Peru is available for thorough study, either from the standpoint of distribution or segregational variability.

*Hevea guianensis* var. *marginata* is questionably known from Peru, by a collection made by Skutch *(No. 4986)* from Curaray, Rio Napo. Many specimens of this variety from Manaos have been examined and found to have the lepidote condition and, on rare occasions, the disk development of *H. pauciflora.* The somewhat revolute leaflet edges appear superimposed on what otherwise seems to be *H. guianensis* with obovate leaflets, rounded at the tip. In these characters (disk is not known) and in superficial aspect the Peruvian collection agrees. It would appear that the development of *H. guianensis* var. *marginata,* through introgression of *H. pauciflora* into *H. guianensis,* should be taken into consideration. The Manaos material indicates that the more or less stable entity has been derived through hybrid origin.

HEVEA GUIANENSIS var. LUTEA × BENTHAMIANA

*H. Foxii* Huber, in Bol. Mus. Goeldi 7:228. 1913.
*H. glabrescens* Huber, l. c., p. 230, in part.

VERNACULAR NAMES: *ituri* (Peru).

KNOWN NATURAL DISTRIBUTION: Rio Putumayo, Peru-Colombia border and Rio Maranon.

PERU: DEPT. LORETO: Rio Putumayo: Liberia, fl. and fr. Feb. 1911, *Fox s. n.* (SYNTYPE of *H. glabrescens* Huber); Ultimo Retiro, fl. and fr. Oct. 1910, *Fox 7* (TYPE of *H. Foxii* Huber). Rio Marañon: Santa Rosa near Pinglo, st. May 14, 1943, *Russell s. n.*

These specimens morphologically are most closely allied to *H. guianensis* var. *lutea,* with its distinct short-shoot, lack of disk lobes, and very irregular anther whorls. In Fox's Liberia specimen, the anthers are of two sizes, two approaching 1 mm. in length, the others about 0.5 mm. However, these characters are complicated by leaflet pubescence, long reddish floral pubescence, and the bud and calyx lobe acumination, which are definitely characters of *H. Benthamiana.*

Two specimens of Huber's *H. glabrescens* were cited in the original description. Both these Fox collections from Sombra and from Pebas appear to me to be better placed in *H. guianensis* var. *lutea* × *pauciflora.*

It is unfortunate that the Russell specimen from the Rio Marañon is sterile, preventing accurate placement. It is such an unusual specimen that superficially some might think it to be a new species. The presence of short-shoots and other characters indicates to me that it is allied to *H. guianensis* var. *lutea,* but the pubescence of the lower leaflet surfaces is extremely dense, as dense as in the most typical of *H. Benthamiana* specimens. The pubescence, however, is white, a character not too often found in good *H. Benthamiana.* With the exception of *H. Benthamiana,* reported found on the Peru border on the lower Putumayo, *H. Benthamiana* appears actually never to have been collected in Peru, much less as far up on the Marañon as Pinglo. The question arises as to how *H. Benthamiana* characters can arise in *H. guianensis* var. *lutea* specimens so far away from *H. Benthamiana* range. Either *H. Benthamiana* exists along the Peruvian Amazon and Marañon and has been overlooked, or *H. guianensis* var. *lutea* is carrying *H. Benthamiana* germ-plasm which occasionally recombines in certain specimens to show itself rather strongly, as in the Russell specimen. This latter theory at present appears plausible to me. Through comparative morphological studies of the flowers, leaves, stems and short-shoots, and through the great amount of segregational-like variability of *H. guianensis* var. *lutea,* I feel that it may have been derived through interspecific hybridization of *H. guianensis* and *H. Benthamiana.*

According to Fox's notes published with Huber's description, *H. Foxii* produced 75 per cent of the rubber of the Putumayo. This region was again in production during the past war, from which came the "Putumayo Block" and "*rabos de Putumayo*[34]" grades of rubber slightly superior to normal *H. guianensis* var. *lutea.* This better quality rubber, as well as morphological characters, would indicate that the *H. guianensis* var. *lutea* of the Putumayo may have incorporated some of the *H. Benthamiana* rubber quality and more of the other *H. Benthamiana* tendencies than is generally found in other regions.

HEVEA GUIANENSIS var. LUTEA × PAUCIFLORA

*H. glabrescens* Huber in Bol. Mus. Goeldi 7:230. 1913, in part.

In morphological aspect the following specimens are most closely referable to *H. guianensis* var. *lutea:*

VERNACULAR NAMES: *jebe debil, jebe debil debil, jebe debil bananera* (Peru).

KNOWN NATURAL DISTRIBUTION: *Tierra altura,* probably in secondary growth, scattered along the Rio Putumayo and the Rio Amazonas, from Iquitos to Caballo Cocha.

PERU: DEPT. LORETO: Rio Putumayo: Sombra, fr. Dec. 24, 1910, *Fox s. n.* (SYNTYPE of *H. glabrescens* Huber). Rio Amazon: Rio Nanay, Tierra Doble, st. June 1929,

[34]Literally translated from the Spanish as "Putumayo tails," used during the past rubber boom as a term describing tail-like appearing masses in the classification of a rubber from that region of Peru. These so-called "Putumayo tails" are made up of scrap rubber, taken from the tapped trees, and is wrapped into shapes simulating tails. Before the use of the more modern tapping knives came into effect, trees were tapped with a small hatchet known as the *machadiño.* In the Putumayo area, coagulated rubber from these wounds was placed in a crude press to form huge masses or "blocks" of rubber, known as "Putumayo blocks."

*Llewelyn Williams 918*, Pebas, st. Mar. 4, 1911, *Fox s. n.* (PARATYPE of *H. glabrescens* Huber); Caballo Cocha, Quebrada Mazamore Cana, st. Oct. 1943, *Seibert 1867*, fl. *1868*.

These specimens all show remarkable similarity to the one syntype of *H. glabrescens* collected by Fox at Sombra on the Rio Putumayo. They are referable to *H. guianensis* var. *lutea*. However, the way in which the peduncle departs horizontally from the short-shoot and hangs down, the short-shoots, leaflet persistence, and the lepidote condition of the under-leaflet surfaces all show *H. pauciflora* tendencies. The latex and rubber quality are poor and as ascribed to *H. guianensis* × *pauciflora*.

The following specimens are most closely referable to *H. pauciflora*, with indications that they are members of an hybrid swarm in which segregation and natural selection are such as to produce types most closely simulating *H. pauciflora*.

*H. paludosa* Ule, in Engl. Bot. Jahrb. 35:666. 1905.
*H. humilior* Ducke in Archiv. Jard. Bot. Rio de Janeiro 5:154, *pl. 20, fig. 50*. 1930.

KNOWN NATURAL DISTRIBUTION: On *tierra altura*, but on the edges and near local marshy areas of pasture land containing second growth and in second growth in the vicinity skirting Iquitos (pl. 44).

PERU: DEPT. LORETO: Iquitos: Estrada Morona, marshy land, outskirts of city, fl. Nov. 1942, *Baldwin 2812, 2813*, fl. and fr. *2814;* road to Morona Cocha, fr. Nov. 1945, *Ducke 1774*, fl. and fr. Oct. 1927, *Ducke 20602* (SYNTYPE-2 of *H. humilior* Ducke), fl. March 1924, *Kuhlman 1526* (Jard. Bot. Rio *No. 2411*), (SYNTYPE-1 of *H. humilior* Ducke), fl. July 1902, *Ule 6260* (TYPE of *H. paludosa* Ule); vic. Punchana, fl. and fr. Sept. 1943, *Seibert 1838*, fl. *1839;* San Juan, st. Dec. 1942, *Baldwin 2819;* Mishuyacu, fl. Oct.-Nov. 1929, *Klug 128*.

These trees, up to 20 m. in height, appear to have a variable range of flowering time. From the presence of both maturing fruit and flowers on the same tree, it would seem that the trees may flower more than once a year. There is some bud acumination, usually an irregularity of the anther whorls, less than 10 anthers, and a reddish tinge to the floral pubescence—all indications of *H. guianensis* var. *lutea*. The calyx lobes always show calloused tips, the peduncle departs at right angles from the stem and droops, and the vein tips are usually calloused and stop short of the blade tip—all strongly indicating *H. pauciflora*. The leaflet scales intergrade between the type of the two entities. The rubber, where known, is always very poor and resinous, turning black when drying.

As in the case of Kuhlman's syntype of *H. humilior*, it is not always too easy to distinguish morphological characters of *H. guianensis* var. *lutea* except in a rather vague way through pubescence characters. Furthermore, the leaflets tend to be more horizontal than erect, so strongly do these members of the hybrid swarm tend towards *H. pauciflora*.

HEVEA GUIANENSIS var. LUTEA × PAUCIFLORA × BRASILIENSIS

PERU: DEPT. LORETO: Rio Ampiyacu, Puca Orquillo, fl. and young fr. Oct. 1943, *Seibert 1862*.

This specimen has caused me considerable concern because it shows morpho-

logical influence of all three species, but, in general, it perhaps most closely simulates *H. guianensis* var. *lutea* on the basis of the erect leaflets, the short-shoots, 8 or less anthers in two whorls, and the vein pubescence of the lower leaflet surfaces. The inflorescence is intermediate between *H. pauciflora* and *H. brasiliensis* while the way in which the peduncle of the young infructescence departs from the stem is that of *H. pauciflora.* The leaves, which persist until after inflorescence maturation and the appearance of the new flush, appear as those found in *H. pauciflora.* The flowers, through acumination and pubescence, are superficially those of *H. brasiliensis,* even to the slight bud contortion. The calyx lobes lack the calloused tips of either *H. brasiliensis* or *pauciflora.* The presence of disk lobes in the pistillate flower simulates those of *H. pauciflora.* The leaflets are quite intermediate between *H. guianensis* var. *lutea* and *H. brasiliensis.* It is interesting to note that the male buds always absciss before anthesis. Perhaps this is a type of male sterility.

The tree was rather small, 15 m. tall, growing on a low hillside well above inundation level. It came from an area where *H. guianensis* var. *lutea* predominates and is known as *jebe debil fino de altura,* yet the rubber from this tree appeared to be quite inferior. The cream-colored latex stains the hands red before rapidly oxidizing to black. This blackish oxidation of the latex is a character which in my experience always shows up where admixture of *H. pauciflora* is suspected.

## Economic Aspects of Current Investigations

Langford (1945) has shown that within the native habitat of the commercially grown *H. brasiliensis* there are strains which naturally resist the virulent South American Leaf Blight, *Dothidella Ulei* P. Henn. Notably resistant strains have been found to exist in the Acre territory of Brasil and from the Leticia region of Colombia on the Peruvian border. More recent studies have included the region of northeastern Madre de Dios, Peru, within the range of resistant *H. brasiliensis* strains.

Living material from these areas is now being grown and tested at various Latin American cooperative experiment stations, on the basis of which it is now possible to develop a sound industry of commercially grown rubber in this hemisphere. Since the South American Leaf Blight exists in many of the Latin American countries and threatens to spread to those in which it has not yet been reported, the development of this natural rubber industry is being based on material naturally resistant to the disease.

Although clones of *H. brasiliensis* have been developed in the Far East which have proved to be of superior yield, none of them have withstood resistance tests against this disease. As a temporary means of utilizing the high-producing, but susceptible, Oriental Clones in the trial plantings within this hemisphere it is necessary to top- or crown-bud these plants with indigenous clones of proven

resistance to the Leaf Blight (Sorensen, 1942). Clones for top budding may include resistant strains of other species than *H. brasiliensis.*

Thus far, time has been a limiting factor in testing and proving yield potentialities of more than a comparatively few of the earlier-found resistant clones. It would seem likely that through large-scale testing of many jungle-selected clones, particularly from superior yielding trees from such promising areas as Madre de Dios and adjoining Acre and Pando, a number of clones will prove to have naturally inherent characteristics of combined superior yield and high resistance. Seedling progeny from seed collected in such areas are growing to maturity at various stations. From these progeny further desired selections may be made and may prove even better than actual individual jungle selections. In addition to these methods of obtaining desirable planting material for Latin America, a breeding program is under way. By artificial breeding it is possible to utilize and combine desired characters of many clones. It is necessary that these clones meet specified requirements of many localities throughout Latin America where the growing of *Hevea* as an additional small farm cash crop would be of benefit to the community.

*Hevea brasiliensis,* as we are beginning to understand it throughout its very large range in the Amazon Valley, is an extremely variable species. It is variable not only in its morphology, but in its habitat preferences, altitudinal range, dry-season tolerance, disease resistance, latex yield, rubber quality and many other specialized features. It becomes apparent along modern lines of genetic thought that within this species itself are the basic ingredients for breeding artificial clonal material suitable to many of the varied conditions found throughout Latin America. For example, the fact that dense human populations and small-farm communities are more or less confined to elevations above the hot, insect-infested lowlands in which *Hevea* is considered to grow best, need not mean that human populations must be moved to *Hevea*-growing areas. It should be the aim, since high-elevation stock is available, to develop *Hevea* so it can be taken to the populations existing between 2000 and 4000 feet, or even higher.

Though natural hybrids between many of the species are recognized, we do not know much more about them than that there appear to be few genetic barriers between the various species.

No species has yet been found to have superior yield of rubber to that of *H. brasiliensis.* Where known, hybrids between it and any other species appear to result in a considerable lowering of qualities which are of prime commercial importance. Indiscriminate or promiscuous interspecific hybridization, if not controlled, could well lead to expenditures of huge sums of money and disastrous results. There are, however, a number of features of some other species such as exceptional disease resistance in strains of *H. pauciflora* and certain other species, the xerophytic nature of some forms of *H. nitida,* and many others which hold an interesting problem of interspecific hybridization for the plant breeder in the improvement of plantation *Hevea.*

## LIST OF PERUVIAN AND BOLIVIAN SPECIMENS STUDIED

Archer, W. A. *7582 (H. nitida); 7583 (H. guianensis* var. *lutea).*

Baldwin, J. T., Jr. *2800, 2801, 2802, 2803, 2805, 2806 (H. pauciflora); 2807 (H. brasiliensis × pauciflora); 2808, 2809 (H. pauciflora); 2810, 2811 (H. brasiliensis × pauciflora); 2812, 2813, 2814 (H. guianensis* var. *lutea × pauciflora); 2815, 2816 (H. pauciflora); 2817 (H. brasiliensis × pauciflora); 2818 (H. pauciflora); 2819 (H. guianensis* var. *lutea × pauciflora); 2820 (H. pauciflora); 2821 (H. brasiliensis); 2822, 2823, 2824, 2826, 2827 (H. guianensis* var. *lutea); 2828 (H. brasiliensis); 2829 (H. brasiliensis × guianensis* var. *lutea); 2829-A (H. guianensis × pauciflora); 2830 (H. pauciflora); 2955, 2957 (H. brasiliensis); 2961 (H. guianensis* var. *lutea); 2998 (H. brasiliensis).*

Buchtien, Otto. *1622 (H. brasiliensis × guianensis* var. *lutea).*

Carpenter, J. B., & Manuel Lescano. *s. n.* P-A[35], P-B, P-1, P-24, P-25, P-26, P-36, P-39, P-52, P-56, P-58, P-65, P-66, P-67, P-69, P-73, P-76, P-77, P-78, P-80, P-81, P-83, P-84, P-85, P-86, P-87, P-88, P-90, P-91, P-99 *(H. brasiliensis);* P-127, P-128, P-129, P-130, P-131 *(H. brasiliensis × guianensis* var. *lutea);* P-142 *(H. brasiliensis);* P-143 *(H. brasiliensis × ?nitida);* P-145, P-146, P-147 *(H. brasiliensis);* P-151, P-153 *(H. guianensis* var. *lutea).*

Ducke, Adolfo. *1774 (H. guianensis* var. *lutea × pauciflora); 20598 (H. guianensis* var. *lutea); 20602 (H. guianensis* var. *lutea × pauciflora).*

Fletcher, Claude. *s. n. (H. brasiliensis); s. n. (H. guianensis* var. *lutea).*

Fox, W. *7,* Herb. Rio *11845 (H. guianensis* var. *lutea × Benthamiana);* Herb. Rio *11847 (H. guianensis* var. *lutea × pauciflora);* Herb. Rio *11848 (H. guianensis* var. *lutea × Benthamiana);* Herb. Rio *11849 (H. guianensis* var. *lutea × pauciflora).*

Hodge, W. H. *6013 (H. brasiliensis × guianensis* var. *lutea).*

Huber, J. *1377 (H. guianensis* var. *lutea); 1534 (H. nitida).*

Killip, E. P., & A. C. Smith. *25406 (H. brasiliensis × H. guianensis* var. *lutea); 28706 (H. guianensis* var. *lutea); 29919 (H. pauciflora).*

Klug, G. *128 (H. guianensis* var. *lutea × pauciflora); 812 (H. brasiliensis × pauciflora).*

Krukoff, B. A. *1628 (H. nitida); 10824 (H. brasiliensis × guianensis* var. *lutea).*

Kuhlman, J. G. *1526 (H. guianensis* var. *lutea × pauciflora); 1527 (H. brasiliensis × pauciflora).*

Langemack, Victor. *s. n. (H. guianensis* var. *lutea).*

La Rue, C. D. *s. n. (H. brasiliensis); s. n. (H. brasiliensis × guianensis* var. *lutea); s. n. (H. guianensis* var. *lutea).*

Rusby, H. H. *885 (H. brasiliensis).*

Russell, Raymond. *s. n. (H. brasiliensis); s. n. (H. guianensis* var. *lutea); (H. guianensis* var. *lutea × Benthamiana).*

Seibert, R. J. *1838, 1839 (H. guianensis* var. *lutea × pauciflora); 1840, 1841, 1842, 1843, 1844 (H. brasiliensis × pauciflora); 1847 (H. brasiliensis × guianensis* var. *lutea); 1848 (H. guianensis* var. *lutea); 1849 (H. brasiliensis × guianensis* var. *lutea); 1850 (H. guianensis* var. *lutea); 1851 (H. guianensis × pauciflora); 1853 (H. brasiliensis); 1854 (H. guianensis* var. *lutea × pauciflora); 1855, 1856, 1857 (H. guianensis* var. *lutea); 1861 (H. brasiliensis); 1862 (H. guianensis* var. *lutea × pauciflora × brasiliensis); 1864 (H. brasiliensis); 1867, 1868 (H. guianensis* var. *lutea × pauciflora); 1869, 1872, 1873, 1874, 1876, 1877, 1882, 1883, 1884, 1893, 1904, 1905, 1923, 1925, 1926, 1932, 1933, 1934, 1935, 1936, 1937, 1938, 1939 (H. brasiliensis); 1940 (H. brasiliensis × pauciflora); 1943 (H. guianensis* var. *lutea); 1944, 1955, 1956, 1957, 1958, 1959, 1960, 1961, 1962, 1963, 1964; 1965, 1974, 1975 (H. brasiliensis); 1978 (H. guianensis* var. *lutea); 2021, 2023, 2024, 2025, 2026, 2027, 2028, 2030, 2031, 2032, 2033, 2053, 2060, 2062, 2065 (H. brasiliensis); 2074, 2078 (H. guianensis* var. *lutea); 2082 (H. brasiliensis); 2087 (H. guianensis* var. *lutea); 2091, 2102, 2105, 2106, 2115, 2116, 2120, 2130, 2141, 2142, 2143,*

[35] Collectors' number lacking, these being references to the clone number of the plant collected. The clones represent jungle selections from Peru cultivated at the Estación Experimental Agricola de Tingo Maria, Peru, where they are undergoing experimental testing.

*2144 (H. brasiliensis); 2184, 2185 (H. guianensis* var. *lutea); 2186 (H. brasiliensis × guianensis* var. *lutea); 2234, 2236, 2261, 2262 (H. guianensis* var. *lutea); 2269 (H. guianensis × pauciflora); 2370, 2371, 2404, 2406, 2407, 2426 (H. guianensis* var. *lutea).*

Seibert, R. J., & Manuel Lescano. *2270, 2271, 2272, 2273, 2274, 2275, 2276, 2277, 2278, 2279, 2280, 2281, 2282, 2283, 2284, 2285, 2286, 2287, 2288, 2289, 2290, 2291 (H. brasiliensis).*

Seibert, R. J., & Raymond Russell. *1881 (H. brasiliensis × guianensis* var. *lutea).*

Skutch, A. F. *4963, 4966, 4974 (H. guianensis* var. *lutea); 4976 (H. brasiliensis × guianensis* var. *lutea); 4980, 4981, 4983 (H. guianensis* var. *lutea); 4984 (H. brasiliensis); 4985 (H. guianensis); 4986 (H. guianensis × pauciflora); 4987 (H. brasiliensis); 4988 (H. brasiliensis × guianensis* var. *lutea); 4990, 4991, 4992 (H. pauciflora); 4993 (H. brasiliensis × pauciflora).*

Ule, E. *6260 (H. guianensis* var. *lutea × pauciflora).*

White, O. E. *2378 (H. brasiliensis).*

Wier, J. R. *s. n. (H. brasiliensis).*

Williams, Llewelyn. *206 (H. brasiliensis); 818 (H. guianensis* var. *lutea); 889 (H. nitida); 918 (H. guianensis* var. *lutea × pauciflora); 2003, 2176 (H. brasiliensis); 2503 (H. brasiliensis × pauciflora); 2931 (H. brasiliensis).*

Williams, R. S. *1657, 1658, 1659 (H. brasiliensis × guianensis* var. *lutea).*

## Bibliography

Association of Central Experiment Stations (Centrale Proefstations Vereeniging) (1939). Identificatiekenmerken van de Voornaamste in de Praktijk Aangeplante Hevea-cloonen. Java.

Arber, Agnes (1934). The Gramineae. The Macmillian Co., New York.

Aublet, M. F. (1775). Histoire des plantes de la Guiane Françoise. **2**:871–873, *pl. 335.*

Baldwin, J. T., Jr. (1946). Am. Jour. Bot. Suppl. **33**:1s.

———, (1947). Hevea: a first interpretation. Jour. Heredity **38**:54–64.

———, (1947). *Hevea rigidifolia.* Am. Jour. Bot. **34**:261–265.

———, and R. E. Schultes (1947). A conspectus of the genus Cunuria. Leafl. Bot. Mus. Harvard Univ. **12**:325–331.

Bartlett, H. H. (1927). A corky-barked mutation of *Hevea brasiliensis.* Bot. Gaz. **84**:200–207, *illus.*

Bentham, G. (1854). On the north Brazilian Euphorbiaceae in the collections of Mr. Spruce. Hook. Jour. Bot. **6**:368–371.

Blandin, J. J. (1941). Why rubber is coming home. Agriculture in the Americas **1**[4]:1–10, *illus.*

Bobiloff, W. (1931). Color-reactions of latex as a mark of identification of Hevea clones. Archief v. d. Rubberc. **15**:302–308.

Brandes, E. W. (1941). Rubber on the rebound—East to West. Agriculture in the Americas **1**[8]:1–11, *illus.*

———, (1943). Progress in hemisphere rubber plantation development. India Rubber World **108**:143–145, *illus.*

Chamberlain, C. J. (1935). Gymnosperms: structure and evolution. University of Chicago Press, Chicago.

Collins, G. N. (1903). Dimorphism in the shoots of Ginkgo. Plant World **6**:9–11.

Cook, O. F. (1941). Jour. Wash. Acad. Sci. **31**:46–65.

Ducke, A. (1925) Archiv. Bot. Rio de Janeiro **4**:111.

———, (1935). Revision of the genus Hevea, mainly the Brazilian species. Archiv. Inst. Biol. Veg. Rio de Janeiro **2**:217–346. (Reprinted 1939).

———, (1943). Novas contribuçoes para o conhecimento das Seringueiras ("Hevea") da Amazonia Brasileira. Agr. Serv. Florestal Rio de Janeiro **2**:25–43.

Frey-Wyssling, A. (1931). Abnormal leaves of *Hevea brasiliensis* as a clonal characteristic. Archief v. d. Rubberc. **15**:114–124.

———, (1933). Characteristics of tappable buddings of the AVROS clones. *Ibid.* **17**:7–12, *pl. 1–2.*

———, C. Heusser, and F. W. Ostendorf (1932). Identification of young buddings of Hevea. *Ibid.* **16**:51–99, *pl. 1–50, 2 tables.*

Geological Society of America (1946). Geological map of South America. New York.

Hemsley, W. B. (1898). Hooker's Ic. Pl. **6**:*pl. 2570–2577.*

———, (1901). Jour. Bot. **39**:189.

Huber, J. (1906). Ensaio d'uma synopse das especies do genero Hevea. Bol. Mus. Goeldi **4**:620–651.

———, (1913). Novas contribuçoes para o conhecimento do genero Hevea. *Ibid.* **7**:199–281.

Klippert, W. E. (1942). Small farm rubber production. Agriculture in the Americas **2**:48–53, *illus.*

La Condamine, C. M. de (1755). Sur une resine elastique, nouvellement decouverte à Cayenne par M. Fresneau: et sur l'usage de divers sucs laiteux d'arbres de la Guiane ou France Equinoctiale. Mem. Acad. Sci. Paris **1751**:319–333, *illus.*

Langford, M. H. (1945). South American Leaf Blight of Hevea rubbertrees. U. S. Dept. Agr. Tech. Bull. 882.

La Rue, C. D. (1919). Variation in fruits and seeds of Hevea. Verslag van de achtste bijeenkomst van het technisch personeel der proefstations en ambtenaren van het department van landbouw. Medan, Sumatra.

———, (1926). The Hevea rubber tree in the Amazon Valley. U. S. Dept. Agr. Bull. 1942.

Maas, J. G. J. A. (1919). Die bloembiologie van *Hevea brasiliensis*. Archief v. d. Rubberc. **3**:280–312.

Maguire, Bassett (1945). Notes on the geology and geography of Tafelberg, Surinam. Geogr. Rev. **35**:563–579.

Mann, C. E. T. (1940). Improvement in the quality of rubber planting material. The Planter **1940**:332–342.

Michener, C. D. (1946). Notes on the habits of some Panamanian stingless bees (Hymenoptera, Apidae). Jour. N. Y. Ent. Soc. **54**:179–197.

Mueller-Argoviensis, J. (1865). Euphorbiaceae. Linnaea **34**:203–204.

Ostendorf, F. W., and H. Ramaer (1931). On phyllotaxis in Hevea (English abstract). Archief v. d. Rubberc. **15**:437–440.

Oviedo y Valdes, G. F. de (1535). Historia general y natural de las Indias. Madrid.

Paddock, E. F. (1943). On the number of chromosomes in Hevea. Chron. Bot. **7**:412–413.

Parkin, John (1900). Observations on latex and its functions. Ann. Bot. **14**:193–214, *pl. 12.*

———, (1904). The extra-floral nectaries of *Hevea brasiliensis* Muell.-Arg. (The Para Rubber Tree), an example of bud scales serving as nectaries. *Ibid.* **18**:217–226.

Pearson, H. (1912). Trinidad and its rubber. India Rubber World **46**:471–474.

Perry, B. A. (1942). Cytological relationships in the Euphorbiaceae. Va. Jour. Sci. **3**:140–144.

———, (1943). Chromosome number and phylogenetic relationships in the Euphorbiaceae. Am. Jour. Bot. **30**:527–543.

Preusse-Sperber, O. (1916). Die Kautschukzonen Amerikas. Tropenpflanzer **19**:201. 1916.

Ramaer, H. (1935). Cytology in Hevea. Genetica **17**:193–236.

Rands, R. D. (1942). Hevea rubber culture in Latin America. India Rubber World **106**:239–243, 350–356, 461–465, *illus.*

Record, S. J., and R. W. Hess (1943). Timbers of the new world. Yale University Press, New Haven.

Royal Botanic Gardens, Ceylon (1899). Caoutchouc or India Rubber: Its origin, collection, and preparation for the market, etc. Circular 105–168, June.

Schmöle, J. F. (1938). *Hevea brasiliensis* en *Hevea Spruceana*—hybride als onderstam voor oculaties. Archief v. d. Rubberc. **22**:178–181.

———, (1941). *Hevea brasiliensis* and *Hevea Spruceana* hybrids as stock for budgrafts II. *Ibid.* **25**:159–165.

Schultes, R. E. (1944). Caldasia **3**:25–32, *illus.*

———, (1944). *Ibid.* **3**:249.

———, (1945). Estudio preliminar del genero Hevea en Colombia. Rev. Acad. Colomb. de Cien. Exact. **6**:331–338, *illus.*

———, (1945). The genus Hevea in Colombia. Leafl. Bot. Mus. Harvard Univ. **12**:1–19, *illus.*

———, (1947). Studies in the genus *Hevea*. I. *Ibid.* **13**:1–15.

Schurz, Wm. L., O. D. Hargis, C. F. Marbut, and C. B. Manifold (1925). Rubber production in the Amazon Valley. U. S. Dept. Commerce, Trade Promotion Series No. 23.

Seibert, R. J. (1947). The shiringero—Upper Amazon rubber tapper. Agriculture in the Americas **7**:43–45, *illus.*

s'Jacob, J. C. (1931). Proeven over kunstmatige kruis-en zelfbestuiving bij *Hevea brasiliensis*. Archief v. d. Rubberc. **15**:261.

Sorensen, H. G. (1942). Crown budding for healthy Hevea. Agriculture in the Americas **2**:191–193.

Tate, G. H. H. (1930). Notes on the Mount Roraima region. Geogr. Rev. **20**:53–68.

———, and C. B. Hitchcock. (1930). The Cerro Duida region of Venezuela. *Ibid.* 31–52.

Ule, E. (1905). Kautschukgewinnung und Kautschukhandel am Amazonenstrome. Beiheft, Tropenpflanzer **6**:1–71. 1905.

———, (1914). *Hevea brasiliensis* im überschwemmungsfreien Gebiet des Amazonenstromes. Bot. Jahrb. **50**; Beiblatt 114:13–18.

## General Index



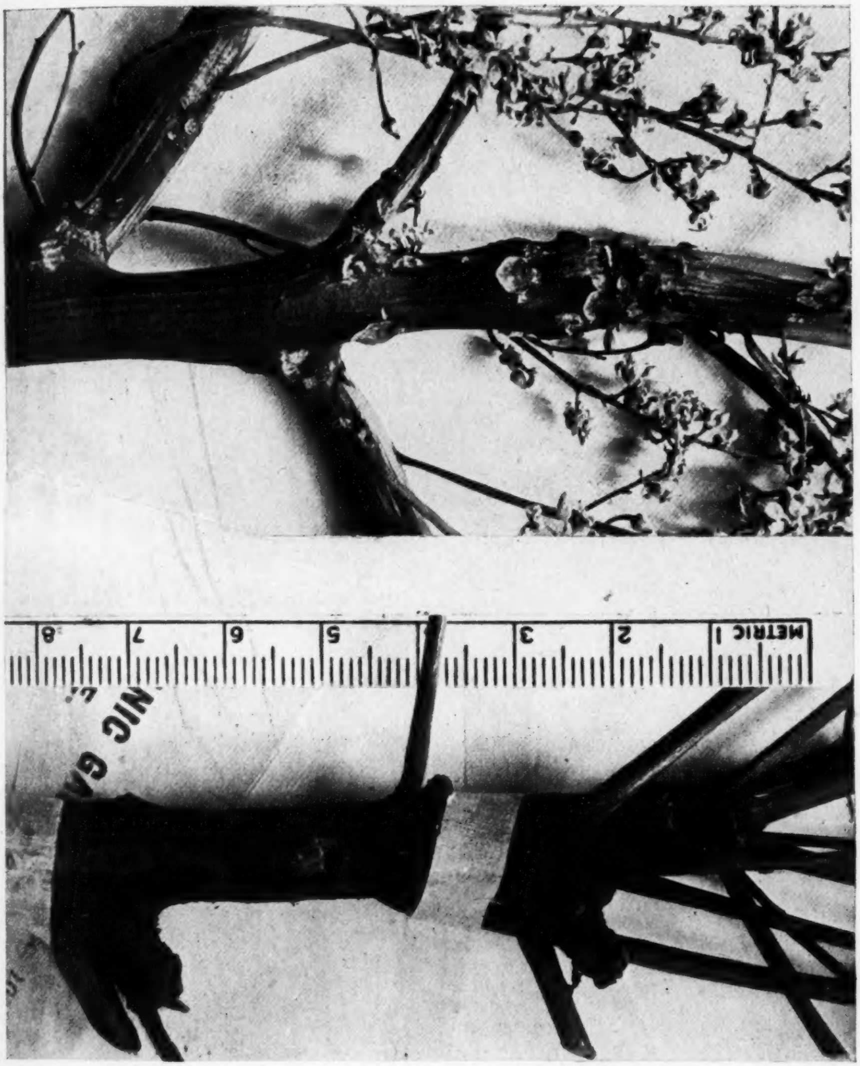
* Valid names are in Roman type, synonyms in *italics*.

## Explanation of Plate

### PLATE 32

Fig. 1. *Hevea brasiliensis.* Terminal and lateral branch growth intervals or "flushes", separated by a narrow ring of bud-scale scars.

Fig. 2. *Hevea pauciflora.* Terminal and lateral branch growth intervals or "flushes", separated by a conspicuous "interflush" short-shoot region. Note the conspicuous lateral spur development preceding long-shoot or "flush" development.



1 SEIBERT—HEVEA IN PERU 2

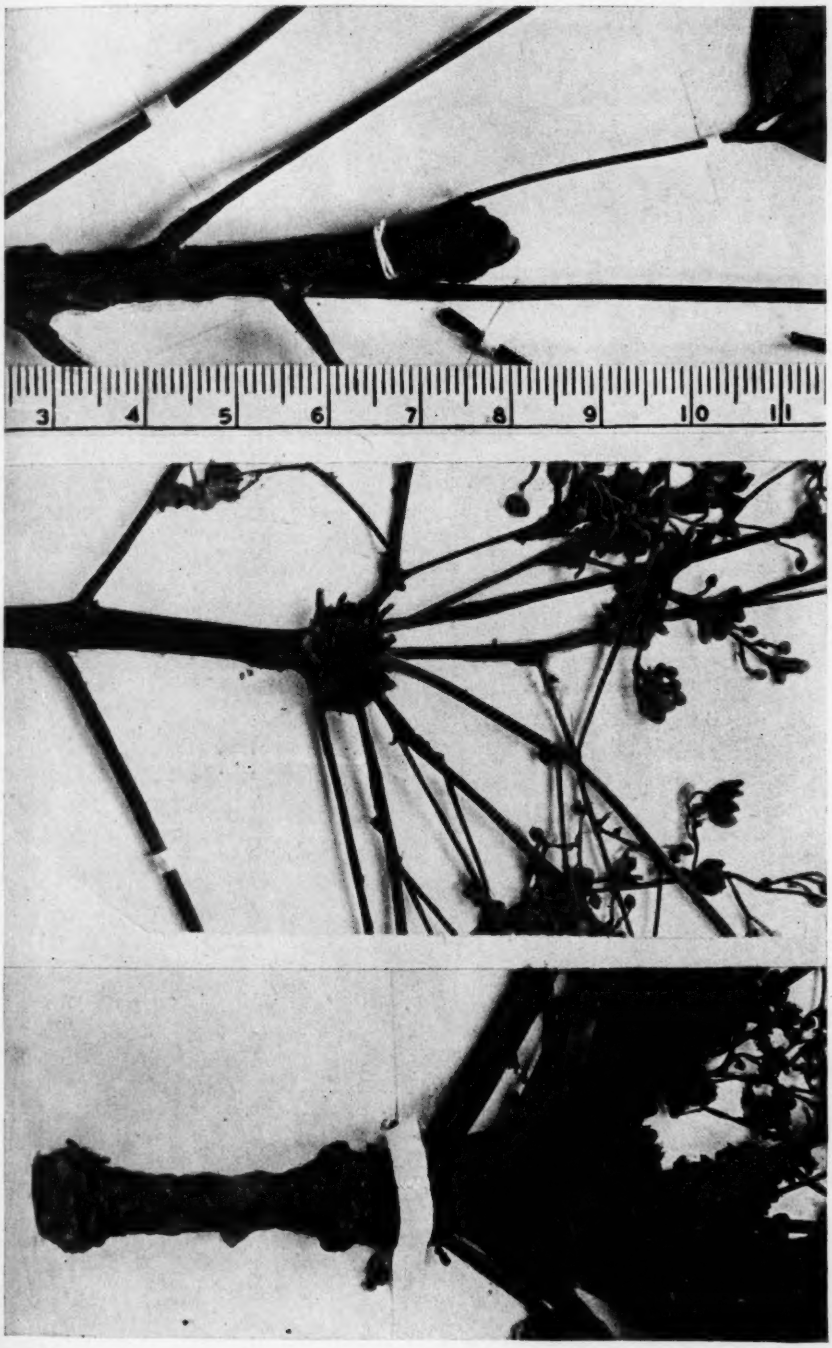
## Explanation of Plate

### PLATE 33

Fig. 1. *Hevea guianensis.* Terminal bud scales and conspicuous development of the short-shoot before the appearance of the inflorescence.

Fig. 2. *Hevea Spruceana.* Terminal bud scales and the short-shoot from which the inflorescence arises.

Fig. 3. *Hevea guianensis.* Three "interflush" short-shoots, from the youngest of which the inflorescence arises. Note the two "flush" regions, upon the upper of which the leaves remain persistent even after the appearance of the new inflorescence.



1

2

3

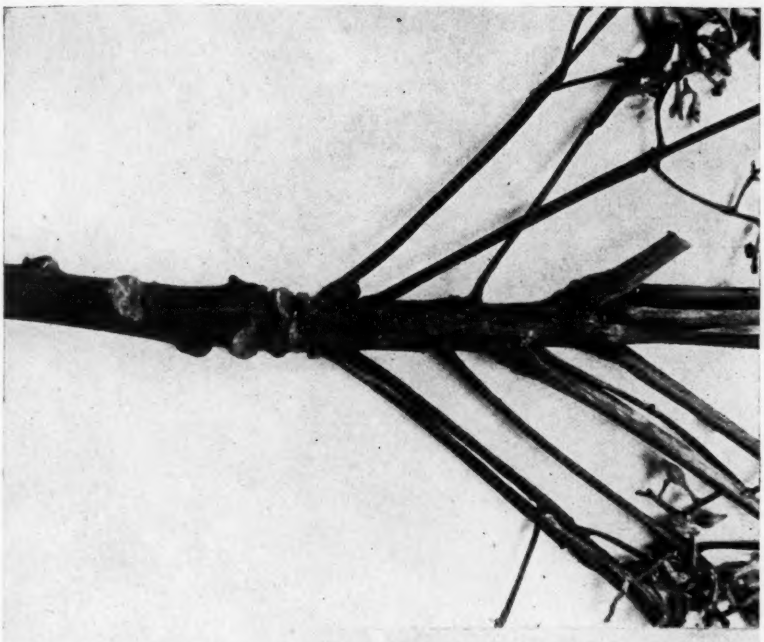
SEIBERT—HEVEA IN PERU

## Explanation of Plate

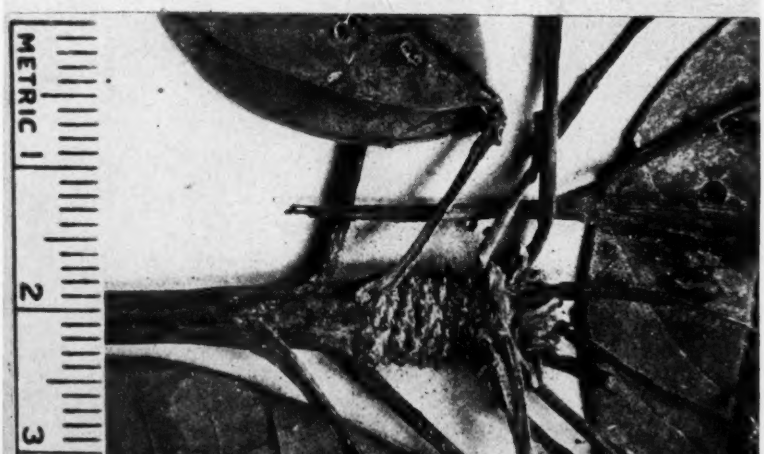
### PLATE 34

Fig. 1. *Hevea brasiliensis.* Complete leaf defoliation of the previous "flush" before the appearance of the inflorescence and new "flush".

Fig. 2. *Hevea rigidifolia.* Complete leaf persistence of the previous "flush" even after the appearance and maturation of the inflorescence.



1




2

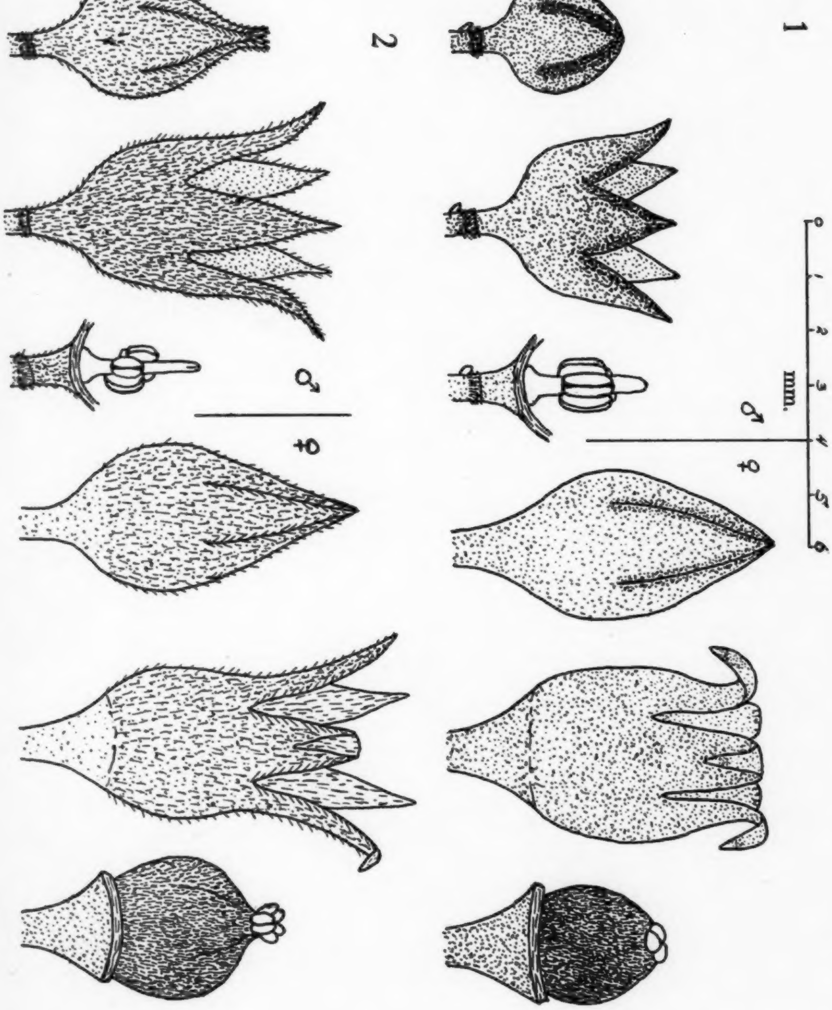
SEIBERT—HEVEA IN PERU

## EXPLANATION OF PLATE

### PLATE 35

Fig. 1. *Hevea guianensis.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.

Fig. 2. *Hevea guianensis* var. *lutea.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.



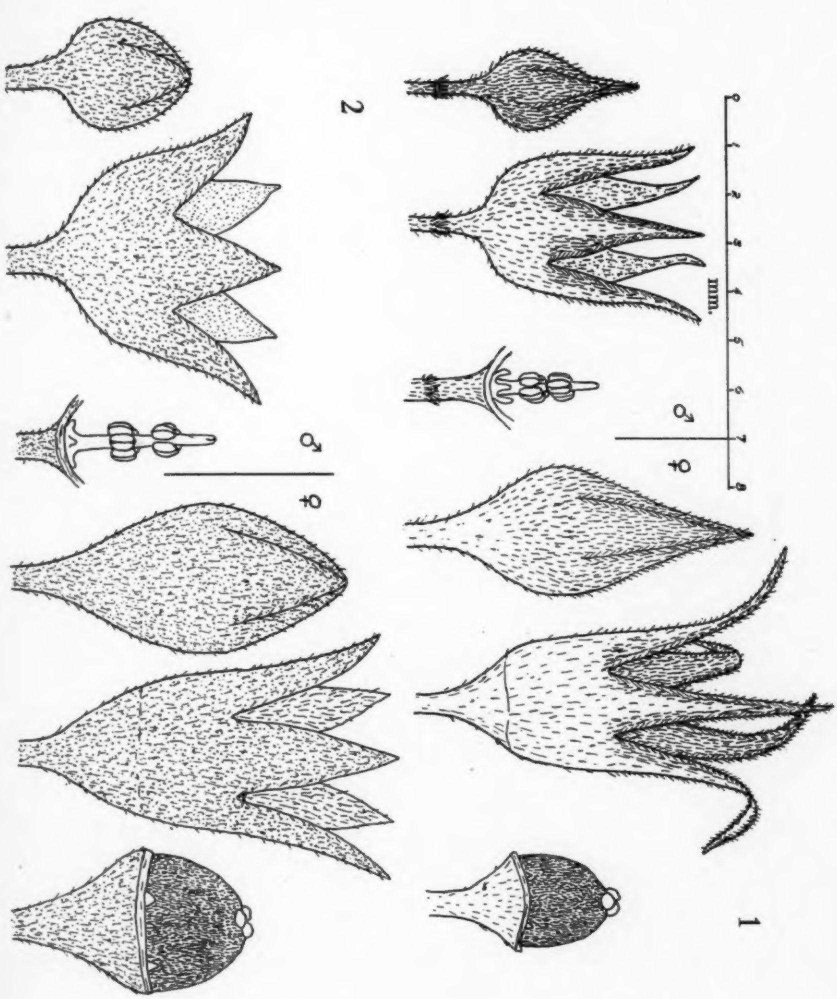

SEIBERT—HEVEA IN PERU

## EXPLANATION OF PLATE

### PLATE 36

Fig. 1. *Hevea Benthamiana.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.

Fig. 2. *Hevea Spruceana.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.



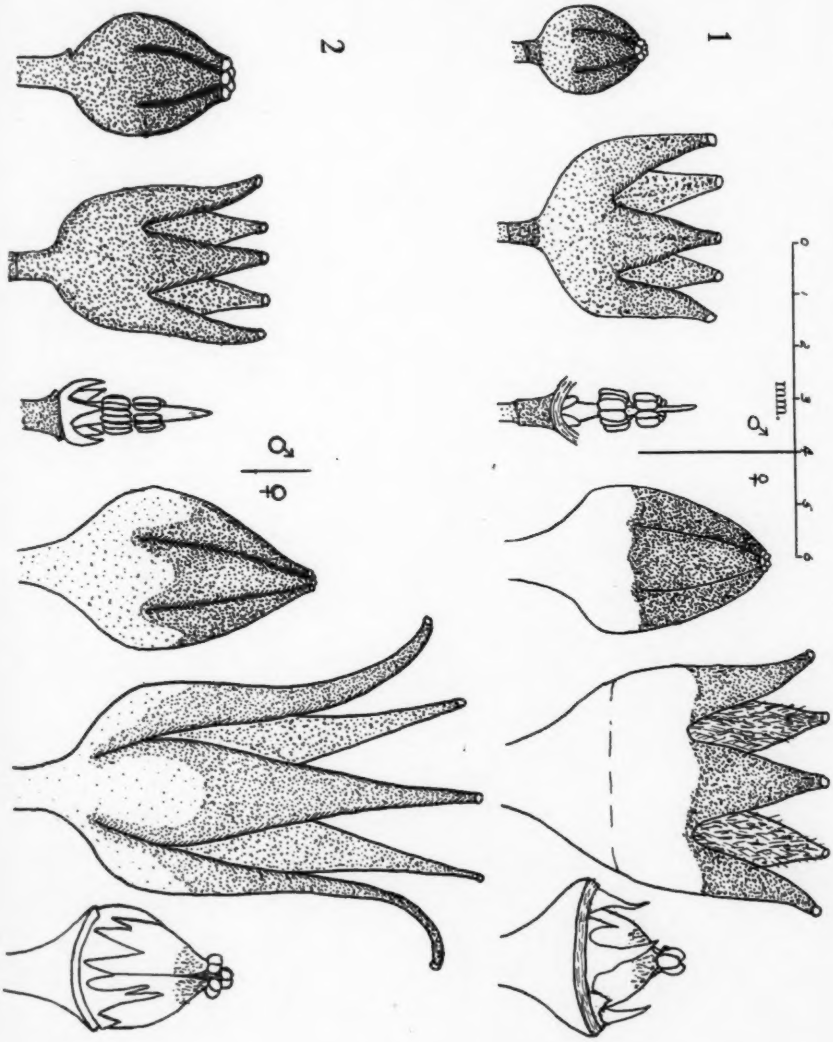

SEIBERT—HEVEA IN PERU

## Explanation of Plate

### PLATE 37

Fig. 1. *Hevea pauciflora.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.

Fig. 2. *Hevea nitida.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.



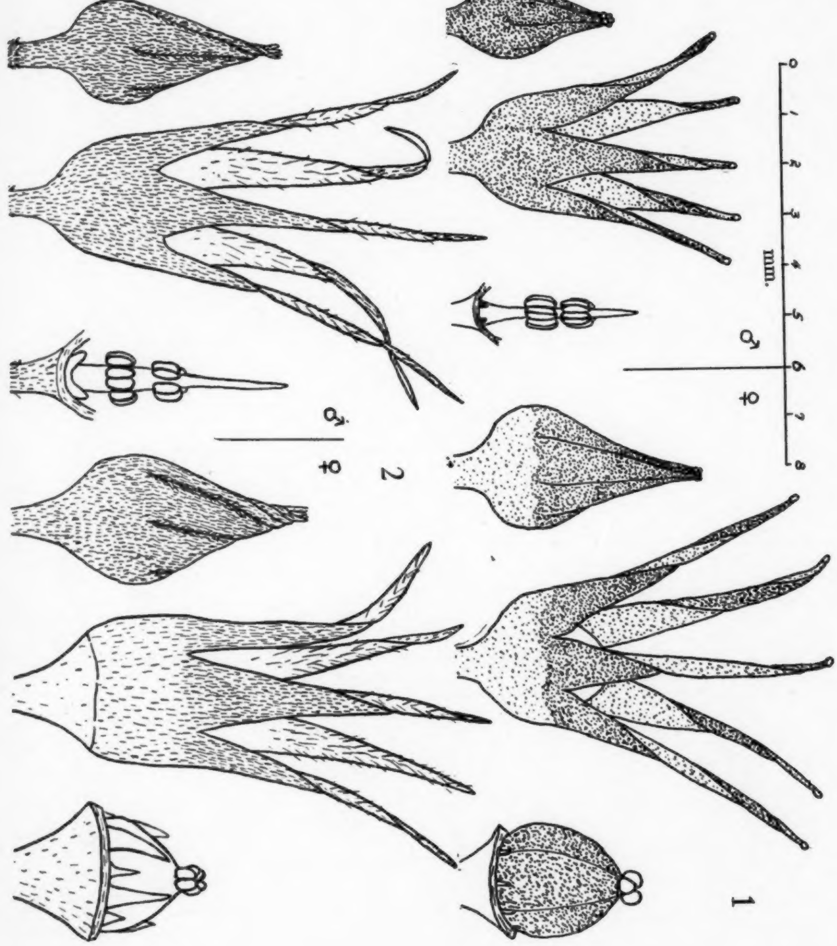

SEIBERT—HEVEA IN PERU

## Explanation of Plate

### PLATE 38

Fig. 1. *Hevea brasiliensis*. Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.

Fig. 2. *Hevea rigidifolia*. Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.

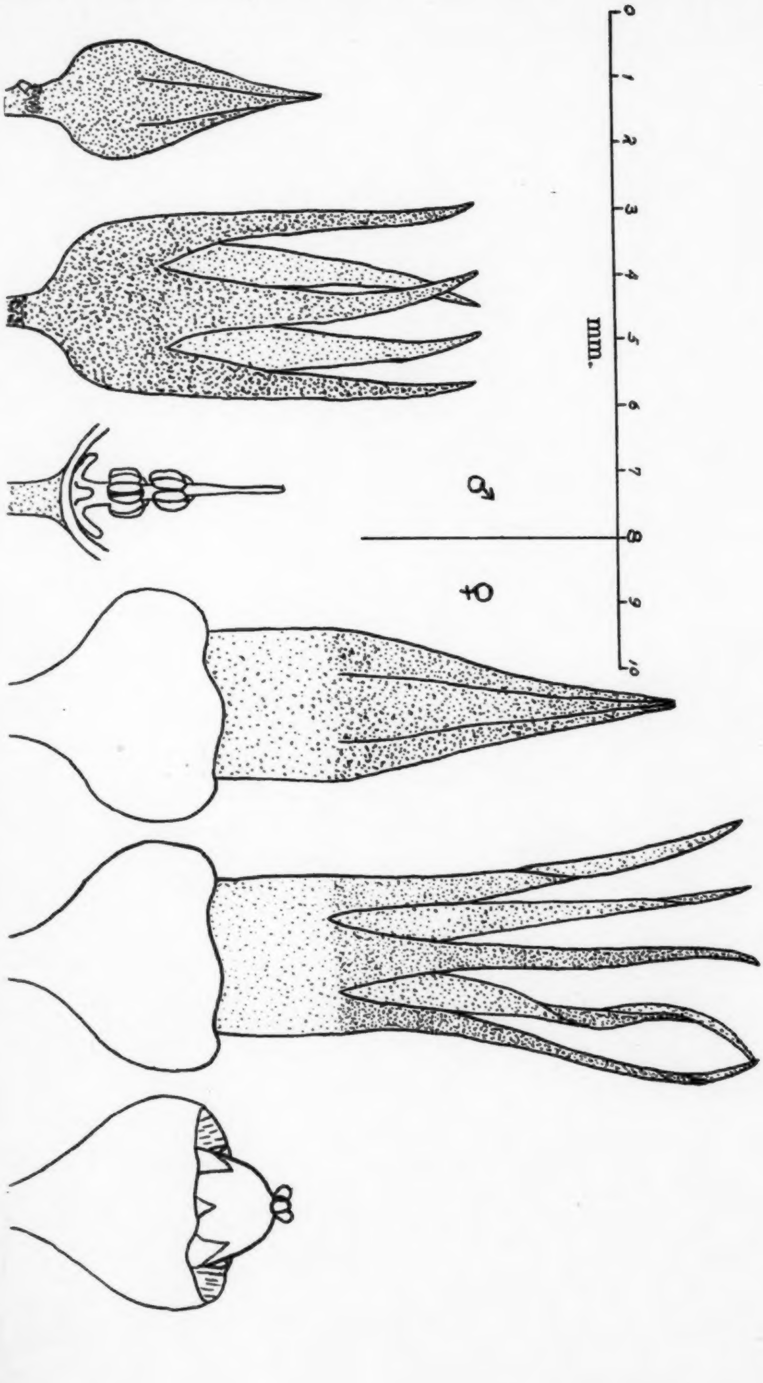



SEIBERT—HEVEA IN PERU

## Explanation of Plate

### PLATE 39

*Hevea microphylla.* Staminate bud, open and dissected flowers; pistillate bud, open and dissected flowers.




SEIBERT—HEVEA IN PERU

## Explanation of Plate

### PLATE 40

Staminate buds above open flowers of the same species.

Fig. 1. *H. guianensis.*

Fig. 2. *H. Spruceana.*

Fig. 3. *H. pauciflora.*

Fig. 4. *H. nitida.*

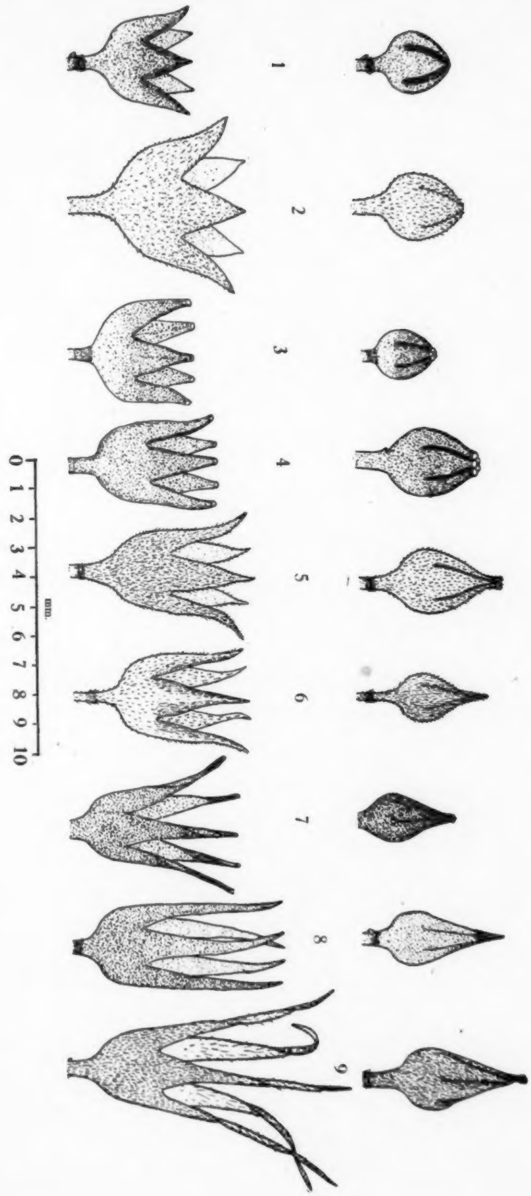
Fig. 5. *H. guianensis* var. *lutea.*

Fig. 6. *H. Benthamiana.*

Fig. 7. *H. brasiliensis.*

Fig. 8. *H. microphylla.*

Fig. 9. *H. rigidifolia.*




SEIBERT—HEVEA IN PERU

## Explanation of Plate

PLATE 41

Pistillate buds above open flowers of the same species.

Fig. 1. *H. guianensis.*

Fig. 2. *H. Spruceana.*

Fig. 3. *H. pauciflora*

Fig. 4. *H. nitida.*

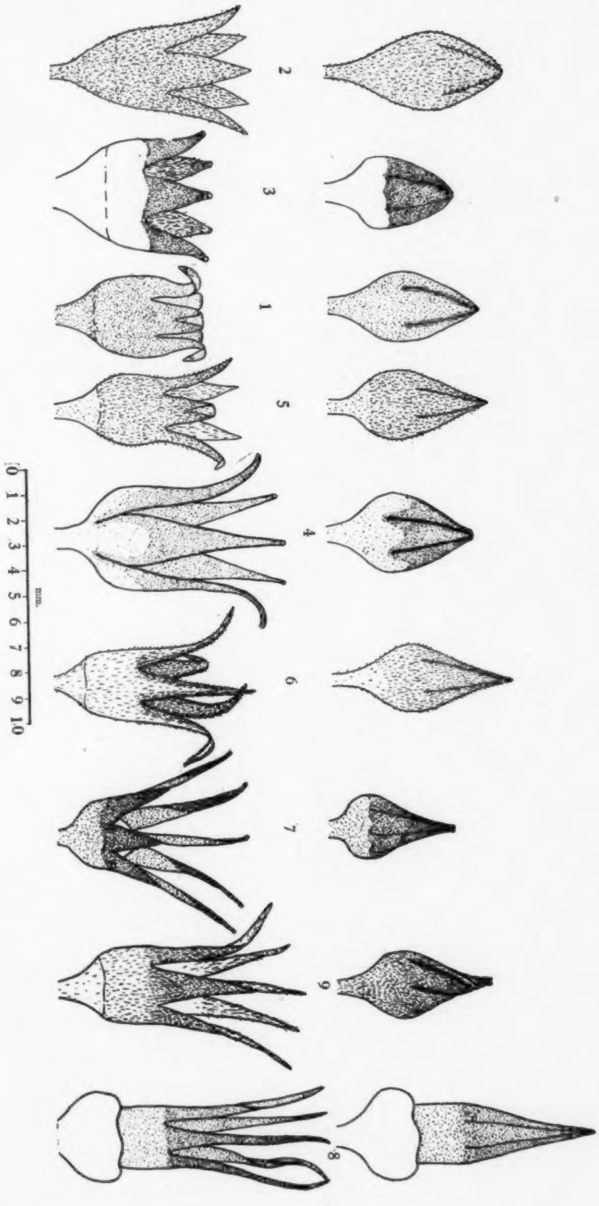
Fig. 5. *H. guianensis* var. *lutea.*

Fig. 6. *H. Benthamiana.*

Fig. 7. *H. brasiliensis.*

Fig. 8. *H. microphylla.*

Fig. 9. *H. rigidifolia.*




SEIBERT—HEVEA IN PERU

## Explanation of Plate

### PLATE 42

Male reproductive organs above female organs of the same species.

Fig. 1. *H. guianensis.*

Fig. 2. *H. Spruceana.*

Fig. 3. *H. pauciflora*

Fig. 4. *H. nitida.*

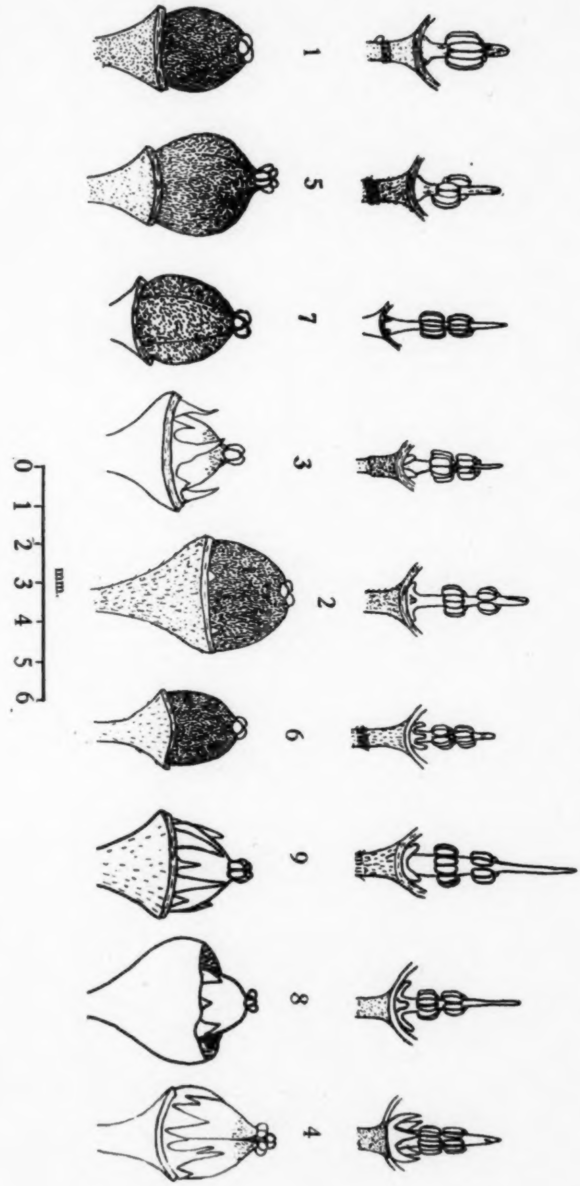
Fig. 5. *H. guianensis* var. *lutea.*

Fig. 6. *H. Benthamiana.*

Fig. 7. *H. brasiliensis.*

Fig. 8. *H. microphylla.*

Fig. 9. *H. rigidifolia.*




SEIBERT—HEVEA IN PERU

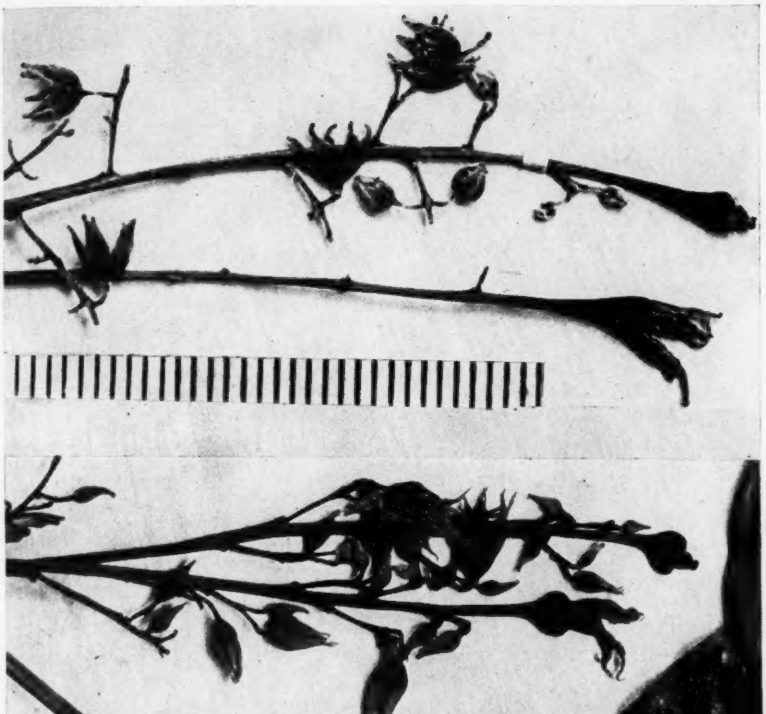
## Explanation of Plate

### PLATE 43

Fig. 1. *Hevea nitida.* Terminal portion of two panicles, showing the terminal pistillate flower with calyx lobes and after calyx-lobe abscission. Note disk lobes at base of ovary. Staminate flowers conspicuously show the calloused calyx lobe tips. Scale in millimeters.

Fig. 2. *Hevea microphylla.* Terminal portion of two panicles, showing the terminal pistillate flower with calyx lobes and after calyx-lobe abscission. Note the conspicuous torus development in this species. Both the staminate and pistillate flowers show the acutely acuminate calyx lobes which are not calloused. Scale in millimeters.

Fig. 3. *Hevea rigidifolia.* Portions of panicles, showing contortion of the bud tips. Scale in millimeters.



1 2 3

SEIBERT—HEVEA IN PERU

## EXPLANATION OF PLATE

### PLATE 44

Changes of natural habitat on outskirts of Iquitos, Peru, made by man through clearing and pasturing. Hybrid swarms of *H. brasiliensis* × *pauciflora* and *H. guianensis* var. *lutea* × *pauciflora* occur in this type of habitat, representatives of which are shown.—Photos by Dr. Richard Evans Schultes.

SEIBERT—HEVEA IN PERU

*Asclepias tuberosa* cl. *tuberosa-interior*